Predator-prey dynamics under variable salinity in the Baltic Sea: the case of an invasive predatory crab, *Rhithropanopeus harrisii* and a native mussel, *Mytilus trossulus*

Essi Kiiskinen

Master's thesis
University of Turku
Faculty of Science and Engineering
Department of Biology
12.5.2020

Ecology and Evolutionary Biology
Credits: 40 ECTS

Referees:

Date of Approval:

Grade:

The originality of this thesis has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

UNIVERSITY OF TURKU
Faculty of Science and Engineering
Department of Biology

KIISKINEN, ESSI: Predator-prey dynamics under variable salinity in the Baltic Sea: the case of an invasive predatory crab, *Rhithropanopeus harrisii* and a native mussel, *Mytilus trossulus*

Master's thesis, 41 p., 3 appendices
Ecology and evolutionary biology
May 2020

Invasive species and other types of environmental change can have antagonistic, synergistic or additive mutual effects and unexpected and irreversible consequences to native communities. Salinity is an important environmental factor for aquatic species, and salinity level that does not fall within the optimal range can cause changes in their morphology. Such changes can also influence the interactions between native and non-native species if they occur in their functional characteristics. My thesis focuses on evaluating whether the Harris mud crab (*Rhithropanopeus harrisii*), a fast spreading non-native species, is affected by the present and future projected salinity variation in the Baltic Sea, and if salinity affects indirectly the predator-prey interaction between the mud crab and the native blue mussel (*Mytilus trossulus*). For this purpose, I monitored growth of claws and body size and survival of adult Harris mud crabs in three salinity levels, which correspond to the salinity in the northern and eastern gulfs of the Baltic Sea (2.5 ppt), in the present distribution range of *R. harrisii* in the Archipelago Sea (5.5 ppt) and in the Baltic proper (7.5 ppt). Due to climate change, salinity of 5.5 ppt may drop to 2.5 ppt in the current distribution areas of the Harris mud crab and 7.5 ppt may retreat from the Baltic Sea altogether. The growth of body size was not affected by salinity, but the growth of male cutter claw height increased in salinity of 7.5 ppt compared to the lower salinities. Therefore, it seems that growth and claw allometry of the mud crab are rather unaffected by the present salinity gradient or predicted salinity decrease in the future. Survival increased with decreasing salinity. In addition to the salinity experiment, the critical blue mussel size for the Harris mud crab was determined. There was a clear relationship between both the claw and body size of the mud crab and its critical prey size – the larger the mud crab, the larger mussel the crab was able to handle. Male Harris mud crabs were able to crush larger prey than females due to their relatively larger claws. The largest blue mussels can reach a size refugia from crab predation but a large part of the blue mussels in the Archipelago Sea are smaller than the size required for refugia and mean mussel size further decreases with decreasing salinity. Lastly, the relation of shell strength and size of blue mussels was evaluated and compared between two populations from differing salinity levels. Mussels from lower salinity had weaker shells in relation to length than mussels from higher salinity. All things considered, unaltered growth and claw allometry along the salinity gradient of the Baltic Sea would mean no effects on the critical prey size and, therefore, no changes in the ecological impact of the invasive predatory crab on mussel populations. However, blue mussels may be more vulnerable to crab predation in low salinities due to smaller size and weaker shells. Overall, this study suggests that the Harris mud crab of the Archipelago Sea is well-adapted to low saline environments and has the potential to spread further to the north-eastern areas of the Baltic Sea.

Keywords: *Rhithropanopeus harrisii*, *Mytilus trossulus*, salinity, invasion, critical prey size, size-selective predation, the Baltic Sea

Contents

1. Introduction

1.1. Global change and invasions of alien species

The environment is changing more rapidly than ever before. Behind the global change is the growing influence of human population. The growth of human population is sustained with agriculture, industries, recreation and international commerce, that are the leading drivers of land transformations, changes in global biogeochemistry and biotic additions and losses (Vitousek et al., 1997). The main components of current global change are increasing atmospheric CO_2 levels and associated climatic changes, deposition of anthropogenically fixed nitrogen (N), loss and fragmentation of natural habitats, and biotic invasions. These environmental alterations have gradually led to dramatic changes in the structure and composition of ecological communities and, furthermore, in global biodiversity and ecosystem processes (Hooper et al., 2005).

Invasions of alien species, i.e. species that occur outside their natural geographic range and dispersal potential (IUCN, 2019), have often been considered as one of the major threats due to global change. Invasiveness is highly context-dependent, but commonly invasive species are opportunistic, tolerant to wide-ranging environmental conditions, have broad diet and high reproductive efficiency and often lack competitors, predators and pathogens that could regulate the expansion of their non-native range (Sakai et al., 2001). Most harmful invasive species displace native species, change community structure and food webs and alter fundamental ecosystem processes, such as nutrient cycling and sedimentation. Marine ecosystems are highly connected via maritime traffic across broad spatial scales and therefore susceptible to introductions. Indeed, international shipping is one of the most significant vectors of alien species (Bax et al., 2003). Species are transported mainly in ballast water and on the hull surface (fouling) from port to port. Increased number, size and speed of ships has enhanced introduction rate of non-native species. Other important vectors are the aquaculture (importations and intentional introductions), the aquarium trade, recreational water users, and the oil, gas and construction industries (Bax et al., 2003).

Most of the organisms carried into new areas do not manage to establish vital populations. They might die during transportation or the new habitat is not suitable for survival, growth or reproduction as various biotic and abiotic factors affect the success of immigrant species (Mack et al., 2000). Some introduced species have become invasive such that their populations seem to grow exponentially and cover increasingly large areas (e.g. Meinesz et al., 2001).

In many cases, the dominance of alien species has been linked to a direct decline of native populations (e.g. Fritts & Rodda, 1998), but sometimes, invasion alone is not enough to explain these ecological changes. The proliferation of alien species can be a result of other forms of environmental change, such as habitat disturbance, which is also the main cause of decline in native populations (Didham et al., 2005; MacDougall & Turkington, 2005). Invasions and other components of environmental change can have antagonistic, synergistic or additive mutual effects and have unexpected and irreversible consequences for native communities (Occhipinti-Ambrogi & Savini, 2003; Occhipinti-Ambrogi, 2007). Invasions can make declining native populations more susceptible to additional environmental changes, and vice versa.

1.2. Invasions of alien predators cause ecological changes in communities

Invasive species may cause an ecological change in native environment, sometimes, with drastic consequences. If the introduced species and the native community do not share evolutionary history, there can be mismatches in ecological interactions between native and non-native species (Verhoeven et al., 2009; Carthey & Banks, 2014). Evolutionary novelty can be beneficial or disadvantageous for either native or non-native species, depending on the mechanism of mismatches in interaction traits (Verhoeven et al., 2009). A non-native species, which is taxonomically distinctive to the local community, has a higher potential to cause severe impacts than taxonomically similar non-native species (Ricciardi & Atkinson, 2004).

Naiveté has the potential to influence any type of antagonistic interactions, but most studies focus on predator-prey interactions (Carthey & Banks, 2014). Naiveté in prey manifests as inability to recognize the novel predation threat and thus failure to adopt effective antipredator responses. In general, alien predators cause greater impact on prey populations than do native predators (Salo et al., 2007; Paolucci et al., 2013). They can cause rapid changes in species composition, abundances and age- or body-size-structures of populations (Goldschmidt et al., 1993; Murray et al., 2007). There can be cascading effects on the whole ecosystem, especially, if the non-native species impacts on local key species of which the whole ecosystem structure is dependent (Matheson et al., 2016). The impacts caused by invasive species are irreversible because a complete eradication of a species is impossible after invasion and establishment.

Brackish water seas, such as the Baltic Sea, are especially prone to introductions of alien species as these species often are highly tolerant to a broad salinity range and local salinity gradient provides them ample opportunities for establishment in different parts of the sea

and, moreover, they benefit from low competition due to low species richness of brackish water seas (Paavola et al., 2005). By year 2012, there were 118 non-indigenous species observed and approximately 90 established in the Baltic Sea (HELCOM, 2012). One of them is the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841). Harris mud crab is native to the Atlantic coast of the North America but has spread as an invasive species to the coasts of the Baltic Sea. Since the first reported encounter in the southern Baltic Sea in 1936 (Schubert, 1936), *R. harrisii* has spread further up north and by 2009 it was encountered in the Archipelago Sea (Karhilahti, 2010). Currently it has established populations along the southwestern coast of Finland and continues to expand its range (Fowler et al., 2013; Forsström et al., 2018). Due to its recent introduction, little is still known about the ecological role of *R. harrisii* in the coastal Baltic communities and its potential to spread further. Previous studies show that it has a potential to alter species-poor littoral communities of the Baltic Sea (e.g. Forsström et al., 2015; Jormalainen et al., 2016; Kotta et al., 2018). To understand the dispersal and the effects of novel predator such as *R. harrisii*, one needs to understand the mechanics behind the interaction between the alien predator and the native prey.

1.3. Growth and size-selective predation by crabs

Crabs (Brachyura) use their claws in foraging, defence and social interactions (reviewed by Mariappan et al., 2000). The right and left hand chelipeds of heterochelous decapods are differentiated to major crusher chela and minor cutter chela, which have different morphology and functionality (Warner et al., 1982). The stronger crusher claw can be used to territorial defence and courtship (Crane, 1975) and crushing hard-shelled prey (Herrick, 1895) while the more agile cutter claw can be used to feeding and grooming (Crane, 1975) or catching (Lang et al., 1978), manipulating and tearing prey (Blundon & Kennedy, 1982). Strong claws are optimal for handling hard-shelled bivalve and gastropod prey. Crab species differ in their shell-breaking abilities (e.g. the strength of the claw closing force) due to varying morphological and biomechanical features of the claws (e.g. Warner & Jones, 1976; Seed & Hughes, 1995; Schenk & Wainwright, 2001). Crabs with weaker and smaller claws use more time on breaking a shell than similar sized crabs with stronger and larger claws (Behrens Yamada & Boulding, 1998; Aronhime & Brown, 2009). Intraspecific variation of crushing ability is strongly size-dependent, meaning that maximum size of a prey, which a given crab can crush (i.e. critical prey size), increases with increasing claw and body size (e.g. Seed, 1980; Boulding, 1984; Milke & Kennedy, 2005). Prey individuals, which exceed the critical size, reach a size refugium, being too large for a crab of a given size to handle.

Brachyuran growth rate is related to moulting rate i.e. the duration of inter-moult phase and growth increment at each moult (McLay, 2015). Growth rate varies depending on body size and sex and is also affected by external factors such as temperature, salinity and food supply (McLay, 2015). Relative growth of claws and body size can be proportionate or disproportionate depending on the type of allometry. Three types of allometric growth exist in brachyurans; (i) positive allometry refers to proportionally higher growth rate of the studied trait with increasing body size, (ii) isometry means equal growth of the trait along body size and (iii) negative allometry means proportionally lower growth rate of the trait with increasing body size (Huxley, 1932). The type of allometry may depend on sex or ontogenetic stage, as in some crab species males' allometric growth of the claws is positive while in juveniles and females it is isometric (Mariappan et al. 2000). Plastic changes in the growth of the chelipeds can be induced by prey (Smith & Palmer, 1994) or parasites (Mariappan et al. 2000). Less is known, how abiotic environmental conditions, particularly salinity, affect the growth of claws and body size. In general, growth of brachyurans tends to decrease in unfavourable salinity conditions (McLay, 2015). A change in morphometrics of claws could influence the ecological role of the crab by changing, for instance, the critical size of hard-shelled prey that a crab can handle. The fact that salinity may affect growth of crab and its claws and therefore affect critical prey size, makes the relationship between claw size and critical prey size an ecologically interesting subject of study. Variation in critical prey size between crab individuals determines the direction of size-selective predation on prey population.

1.4. Physiological salinity tolerance is species-specific

Salinity is one of the most significant environmental factors, which regulate the distribution of species in aquatic environments. Salinity divides aquatic species into three main groups: marine, freshwater and brackish water species. Average salinity in marine habitats is 35 ppt. In freshwater habitats salinity is nearly zero. Brackish water habitats fall between marine and freshwater with salinity of 0.5-35 ppt. While marine and freshwater environments usually have stable salinity levels, brackish water environments can have significant spatial and temporal fluctuations of salinity.

There are constant exchange of water, ions and organic molecules between aquatic organisms and their environment (reviewed in Larsen et al., 2014). Stable intracellular and extracellular salt and water balance is essential to the function of metabolic systems. To maintain cellular function, some species are able to maintain stable osmotic pressure of the internal medium by active ion transportation. This adaptation mechanism is called osmoregulation and it has been

extensively studied in fishes and crustaceans (e.g. Evans et al., 2005; Freire et al., 2008). All species living in fresh or low saline brackish water are osmotic hyper-regulators, which maintain higher osmolarity than their surroundings (Bradley, 2008). To maintain electrolyte balance, hyper-regulators actively absorb ions through appropriate organs, such as gills and excrete dilute urine. Other mechanisms include the reduction of the permeability of the body surface to water and salt or the reduction of osmotic gradient across the body surface to decrease excessive water fluxes (Henry et al., 2012). Organisms which live in higher salinities and have lower osmolarity of internal fluids than their surroundings, are hypo-regulators and increase water intake and excrete excessive ions e.g. via gills or concentrated urine.

Many marine invertebrate species are osmoconformers, which maintain osmotic concentration of their body fluid equal with the environment to minimize water fluxes across membranes (Rivera-Ingraham & Lignot, 2017). Being unable to regulate body osmolarity makes organisms susceptible to all changes in osmolarity of the environment and, therefore, osmoconformers usually have limited tolerance to salinity fluctuations (Larsen et al., 2014). Hard-shelled bivalves can temporarily protect themselves from osmotic stress by closing the valves and isolating from external low salinities (Davenport, 1979). The advantage of osmoconformation compared to osmoregulation is that less energy is needed to ion transport.

Salinity that is higher or lower than the optimal range can cause changes in physiology, behaviour, life history and morphology of aquatic organisms (Grzesiuk & Mikulski, 2006). Organisms need to allocate more energy resources to maintenance of osmotic balance so that their metabolic systems can function properly (Smyth & Elliott, 2016). When more energy is allocated to osmoregulation, less energy is available to other functions, such as growth. The energy available for growth (i.e. the scope for growth) is the difference between the energy gained from consumed food and energy loss to respiration and excretion (Winberg, 1960). Optimal salinity for growth is often highly species-specific (e.g. Kumlu & Jones, 1995; Ruscoe et al., 2004; Ye et al., 2009). Even though the energy required to osmoregulation decreases towards the iso-osmotic point (i.e. the osmotic concentration is equal between the internal fluids of the organisms and the environment) and potentially releases energy to other functions, the growth rate may be highest at lower or higher salinity levels than the iso-osmotic point depending on the species' adaptations. For example, the internal concentration of *Gammarus oceanicus*, the largest amphipod in the Baltic Sea, is iso-osmotic with the ambient salinity at 31.5 ppt (Normant et al., 2005), but the scope for growth is highest at 7 ppt (Normant & Lamprecht, 2006), thus showing a specific adaptation to life in low salinity habitat. While the physiological effects of salinity on organisms are well quantified, few studies have

involved experimental manipulation of salinity in an attempt to assess its role in species interactions.

1.5. Spatial and temporal variation of salinity in the Baltic Sea

Brackish water can be a challenging environment because low and variable salinity limits the distributions of marine and freshwater species, which usually tolerate only a narrow range of salinity and are therefore called stenohaline organisms. Many species find the margin of their salinity tolerance in the Baltic Sea due to low salinities and strong salinity gradient. Low diversity of marine, freshwater and euryhaline species (Elmgren & Hill, 1997) and "dwarf-sized" species (Riisgård et al., 2014) are characteristics to the communities of the Baltic Sea. Salinity decreases gradually from southwestern parts of the Baltic Sea towards northern and eastern gulfs. Surface salinity changes from 16 ppt in the Great Belt to 8 ppt in the southwestern-most part of the Baltic proper and further to 0-3 ppt in the Bothnian Bay and Gulf of Finland (Furman et al., 2014). Furthermore, the Baltic Sea is stratified i.e. salinity increases with depth (Furman et al., 2014). Salinity gradient is generated by freshwater runoff from the land and infrequent saltwater inflows from the North Sea. Although there is seasonal variation in salinity (HELCOM, 2013), the Baltic Sea has rather stable salinity gradient compared to other brackish water environments, such as estuaries. However, salinity is projected to decrease with increasing precipitation and slow rate of saltwater inflows due to climate change (HELCOM, 2013). The magnitude of the potential decrease is uncertain. In a study by Meier and others (2006), salinity change was projected to vary between -45 % and +4 % between 2071-2100. Largest negative change would mean that surface salinity in the Bornholm Basin will be equal to the present-day salinity in the Bothnian Bay. In the models of Vuorinen and others (2015), surface salinity will decrease under 7 ppt in all parts of the Baltic Sea by the end of the century. Border for the surface salinity of 5 ppt will shift from the mid Bothnian Bay southwards to the north of Island of Gotland. According to the report by HELCOM (2013), total decrease would be larger where salinity is highest i.e. the Danish straits while it would be smallest in the less saline areas such as the Bothnian Bay. However, relative decrease of salinity would be largest in less saline areas that could have more profound ecological consequences on local communities.

1.6. The Harris mud crab (*Rhithropanopeus harrisii*) – a recent novel invasive predator in the Baltic Sea salinity gradient

The Harris mud crab is a small-sized (carapace width < 26 mm) predator and scavenger with heterochelous crusher and cutter claw. It has wide diet including algae, amphipods, bivalves, gastropods and detritus (Czerniejewski & Rybczyk, 2008; Czerniejewski, 2009). It is an euryhaline species and can be found in a broad range of salinities (adult individuals at 0.5-41 ppt Boyle et al., 2010). Even though *R. harrisii* is an efficient hyper-osmoregulator, it uses a significant amount of energy to maintain osmotic balance at lower salinity levels than its species-specific iso-osmotic point of 24 ppt (Normant & Gibowicz, 2008; Diamond et al., 1989). When more energy is allocated to osmoregulation, less energy may be available to growth. The effects of salinity on the development of juveniles has been studied extensively (e.g. Costlow et al., 1966; Christiansen & Costlow, 1975) but no studies have been conducted on how variation in salinity affects the growth of adult Harris mud crabs. In the Baltic Sea, the effects could differ locally because mud crabs are exposed to salinity gradient along their distribution range. In addition to spatial differences in salinity, mud crabs may be affected by gradual long-term changes in salinity due to climate change. Altered growth rate could trigger changes in predation efficiency and prey-size preference of Harris mud crabs.

1.7. Blue mussel (*Mytilus trossulus*) – at the margin of the salinity tolerance

Blue mussels (*Mytilus trossulus*) are epifaunal bivalves, which form beds of dense populations by attaching to solid substrates by strong and elastic byssal threads (Silverman & Roberto, 2010). The Harris mud crab of the Baltic Sea feeds on blue mussels among other invertebrates, algae and detritus (Czerniejewski & Rybczyk, 2008). They prefer small and medium sized individuals (Forsström et al., 2015), but studies on the critical size of the Baltic Sea mussels as a prey for non-native *R. harrisii* have not been conducted. In general, the predator-prey relationship between invasive *R. harrisii* and native *M. trossulus* is still poorly understood.

Mussel shell properties such as thickness and shape determine bivalve prey selection of crabs (Mascaró & Seed, 2001; Pickering & Quijón, 2011; Campbell et al., 2019) and are therefore important factors in predation risk of mussels. Blue mussels are relatively small and thin shelled in the Baltic Sea compared to their marine counterparts due to low salinity levels (Kautsky et al., 1990). Distribution of blue mussels is limited to salinity over 4 ppt and therefore they are absent from the Bothnian Bay and the easternmost parts of the Gulf of Finland. Low predation pressure has also been stated to explain small size and thin shells of

blue mussels (Kautsky et al., 1990). When predation risk is low, there is less pressure to invest on thicker shells or higher growth rate. In the southwestern parts of Baltic Sea, blue mussels are preyed by the common starfish (*Asterias rubens* Linnaeus, 1758) and the European green crab (*Carcinus maenas*), while predation pressure in the northern Baltic Sea is far more limited to some bird and fish species (Kautsky, 1981).

The projected decrease in salinity of the Baltic Sea would most likely affect mussels' growth and morphology and shift their distribution range southward from the northern Baltic, where salinity is low and relatively decreases the most. Likewise, predation pressure may change dramatically as *R. harrisii* presents a fast spreading and taxonomically and functionally novel predator type. Decreasing salinity and arrival of a novel predator may affect additively or synergistically blue mussel populations in the Baltic Sea. Little is known about how the predicted changes in salinity might influence the ecological interactions between the Harris mud crab and the blue mussel in the Baltic Sea.

1.8. Study questions and hypotheses

The aim of my thesis is to study how salinity in the Baltic Sea affects the growth of adult Harris mud crabs and, through changes in size and allometry, its predation on native blue mussels of the Baltic Sea. My main hypothesis is that decreasing salinity in space and time decreases the growth of invasive *R. harrisii* and therefore redirects size-selective predation of mud crabs to smaller and/or younger blue mussels. To study this hypothesis, I have two objectives of which the first is to examine the variability of growth with consecutive changes in allometry of claws and survival of Harris mud crabs at different salinity levels present in the Baltic Sea. I expect decreased size increment and moulting rate based in adult mud crabs, which are exposed to unfavourable salinity. Understanding the effects of salinity on growth of mud crabs allows predictions of morphological changes, which mud crabs may go through during invasion to habitats of different salinities and in the course of the predicted change in salinity due to global change. Effects on growth and survival can also be used to evaluate the potential of the Harris mud crab to invade new areas of low salinity in the present and expected future salinity regime of the Baltic Sea.

The second objective is to examine the predator-prey relationship between the non-native Harris mud crab and the native blue mussel by determining the critical size of blue mussels and how it varies with the size of mud crabs and by evaluating blue mussels' morphological characteristics (i.e. morphological dimensions and shell strength), which have a crucial role in

protection against mud crabs. By finding out the critical shell size of mussels and considering the size range of mussels and mud crabs in Archipelago Sea, I will be able to evaluate the size refugium of mussels for crab predation and predict hypothetical impacts of predation on mussel populations in the Archipelago Sea. Also, considering the results of salinity experiment, the consequences of different salinity regimes to the predator-prey relationship between the Harris mud crab and the blue mussel can also be evaluated. Furthermore, my results can be useful when making predictions about the influence of future decrease of salinity in the Baltic Sea on the predator-prey interactions of *R. harrisii* and the blue mussel.

2. Materials and methods

2.1. The effects of salinity on performance of Harris mud crabs

The Harris mud crabs used in the salinity experiment and to analyse allometry of the crabs were sampled in May 2018 from Asemalahti, Seili island in the Archipelago Sea (N60°14'23.7" E21°58'12.3"). Ten mud crab traps (20 × 20 × 20 cm plastic crates filled with autoclaved oyster shells or pieces of claypot) were placed in the depth of 1.3-2 m. Traps were collected after 11 days (from 5th to 16th of May) and caught crabs were measured (n = 131) for carapace width (CW), crusher claw height (CRH) and length (CRL), cutter claw height (CUH) and length (CUL) to ± 0.01 mm with digital calipers (Figure 1) and also wet body weight (BW) to ± 0.01 g. Both adult males (n = 103) and females (n = 28), representing a wide size range (mean CW males 15.19 ± 3.74 mm, range 6.64-20.96 mm; females 11.74 ± 1.26 mm, range 9.81-14.13 mm), were included. Expectedly, carapace width of males was significantly than females (The Exact Wilcoxon Two-Sample Test: $p < 0.0001$).

Crabs were put into individual cradles (Ø 12 cm), which were randomly placed into 24 aquaria (35 × 30 × 30 cm, 24 L) with natural seawater (approx. 5.5 ppt) in the Archipelago Research Institute in Seili, Nauvo (N60°14’ E21°60’). The aquaria were placed in three separate two shelved racks. There were eight aquaria per rack with four aquaria on each shelf. The water of the flow-through circulated through the 300-L reservoir of each rack, from where seawater was pumped up to each aquarium with constant flow and then flowed back via gravity. The water was mechanically and biologically filtered and UV-sterilized (SCHURAN Jetskim 120). Temperature was adjusted gradually to 17 °C and controlled with a cooler system (TECO TR15). Aquarium racks were equipped with four LED lamps (Radion™ XR30w Pro lamps) of which each consisted of two groups of LEDs, one group for each aquarium. Light rhythm was set for 06:00-

19:00 with light intensity gradually increasing to its maximum, then staying there and then gradually dimming to minimum.

Each aquarium rack was assigned to one of three salinity treatment groups: 2.5, 5.5 and 7.5 ppt. These salinities fall within the range found in the Baltic Sea; 2.5 ppt is equivalent to salinity found in the northern and eastern bays of the Baltic Sea, 5.5 ppt is minimum salinity of the present distribution range of *R. harrisii* in the Baltic Sea and salinity of 7.5 ppt represents the Baltic proper. Additionally, they represented salinities after projected decrease of salinity due to climate change. Salinity of 5.5 ppt may drop to 2.5 ppt in the areas covering current northern-most distribution of the Harris mud crab and 7.5 ppt may retreat from the Baltic Sea altogether. Prior to the experiment, there was gradual acclimatization to the salinity change for mud crabs lasting 12 days. Salinity was adjusted by adding sea salt or distilled water into bottom reservoirs. Evaporated water was replaced with distilled water to keep the salinity at fixed level.

I checked the aquaria once a week during which I measured salinity and temperature (pH/mV/C° 110 meter, VWR) and adjusted them if necessary. Each aquarium was also equipped with Onset's HOBO pedant data loggers, which recorded temperature during the experiment. I fed the crabs with fresh Baltic herring, algal pellet and chitin and removed excess algae and food from cradles and aquaria. Those crabs, which had moulted, I measured for carapace width, claw dimensions (CRH, CRL, CUH, CUL) and wet body weight (BW). I also measured dead individuals (only carapace width) and monitored the death date. The experiment lasted for 156 days.

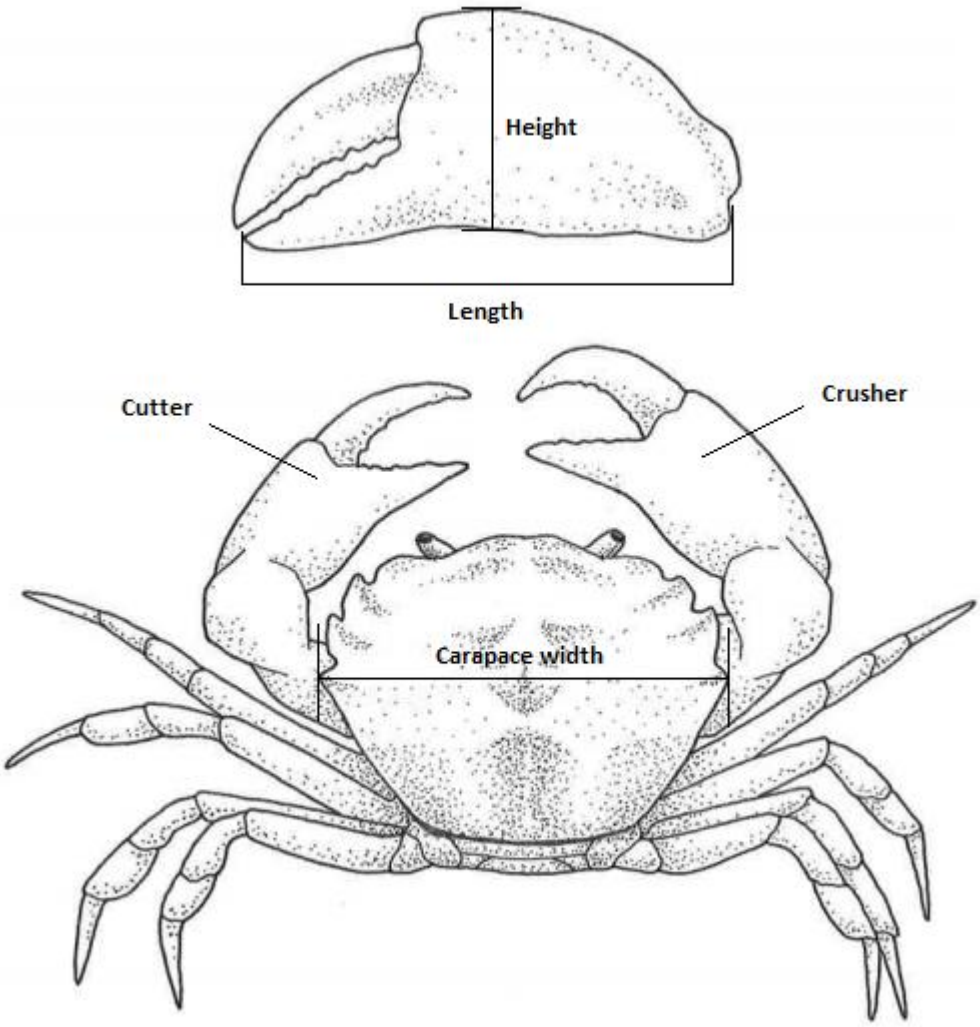

Figure 1. The measurements taken from the specimens of the Harris mud crab (Rhithropanopeus harrisii) in the salinity and critical prey size experiments. Both crusher and cutter claws were measured for height and length.

2.2. Critical size of blue mussels as a prey for the Harris mud crab

Blue mussels used for determination of the critical mussel size were sampled in October 2018 from Päiväluoto, Parainen (N60°15'14" E21°57'52'') and Järvistensaari, Turku (N60°23'06'' E22°07'09''). The Harris mud crabs were sampled during September and October in 2018 nearby Seili, Nauvo (N60°14'23.7" E21°58'12.3"). Ten mud crab traps (20 × 20 × 20 cm) plastic crates filled with oyster shells or pieces of claypot) were placed in the depth of 1-2 m. Caught crabs were collected from the traps three times, once every one or two weeks. Additionally, I collected mud crabs from three similar traps in 19th of October from Tuorla, Kaarina (N60°24'47'' E22°26'37'') In total, 112 crabs (39 females and 73 males) were taken to

aquarium facilities at the University of Turku, where I measured them for carapace width, claw dimensions (CRH, CRL, CUH, CUL) (to ± 0.01 mm) with digital calipers and wet body weight (BW) (to ± 0.01 g). After measuring, I put them individually in 5-dl glass jars with oyster shells as substrate and shelter. Jar size was selected so that crabs were not able to escape from them. I placed 8-10 jars each to aired aquaria (38 × 20 × 25 cm or 45 × 25 × 26 cm) with natural seawater. All in all, there were 12 aquaria and 112 mud crab individuals. Also blue mussels were kept in aquaria (45 × 25 × 26 cm) with aired natural seawater. Temperature was set to 13 °C and light rhythm to 07:00-20:00.

During acclimation period the crabs were fed with fish. Three days before the start of the experiment, they were deprived of food to even their hunger levels. During the experiment, I provided a series of increasingly large mussels to the mud crabs. The experiment was started by giving one mussel for each crab (mussel length 3 mm smaller than the carapace width of each crab). I checked the mussels after 24 h and I recorded whether the mussel had been eaten or damaged. Then I removed the mussel or any remnants of it, and the crab was starved for the next 24 h. Then I added a new mussel, that was 1 mm larger than the previous mussel if it had been eaten or 1 mm smaller if the previous mussel had not been eaten. I continued adding a new mussel and fasting the crabs in 24-hour intervals until each crab ate its first mussel, when the size of the offered mussels was decreasing, or stopped eating any larger mussels. Crabs, which stopped eating I gave a smaller mussel to verify that the crab was still healthy and feeding. If this smaller mussel was intact after 24 h, the crab was excluded from the experiment. I determined the critical prey size (the maximum valve size that mud crabs could crush and open) for each crab as the average size between the smallest mussel that crab was not able to crush and the largest mussel that crab was able to crush. Crabs, which moulted during the experiment I excluded from the data. All in all, 82 crabs (56 males and 26 females, mean CW 14.42 ± SD 3.51 mm, range 8.41 - 21.21 mm) were included in the final data.

2.3. Morphometrics and shell strength of blue mussels

The blue mussels for the morphometric analyses were collected from Luvia (n = 46) (N61°23’23.5’’ E21°25’11.5’’) and Tvärminne (n = 36) (N59°49’54.4’’ E23°14’59.3’’) in mid-August 2018. They were kept in aired containers with natural seawater in laboratory of experimental ecology in University of Turku. I cleaned all epibionts off the mussel shells before measurements. I measured the valve length, width and height (± 0.01 mm) with digital calipers and also wet body weight (± 0.01 g) for individuals of a wide size range. Also, I estimated shell strength for each measured individual as the force needed to cause shell breakage (± 0.01

Newtons). Force was measured with manual force gauge PCE FM 50 (2 mm) by puncturing valves from both sides of the mussel. Puncture point was approximately in the cross section of posterior end of the hinge ligament and centre of the shell (Figure 2). The force needed to break the shell is not necessarily linearly related to the force a mud crab needs to break the shell, because the measuring technique did not resemble the crushing function of a crab. The force was measured around middle of the mussel, while crabs seem to open mussels from the posterior side of the mussel or around the umbo (own observation). While being aware of this restriction, the measuring point was selected because it gave the best repeatability.

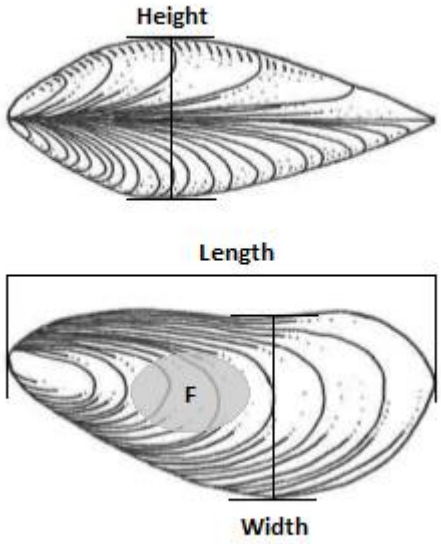

Figure 2. The measurements taken from the specimens of the blue mussel (*Mytilus trossulus*) in the experiments. Grey area marked with F indicates the approximate puncture point for shell strength measurement.

2.4. Statistical analyses

Statistical analyses were conducted with SAS Enterprise Guide 7.1. (SAS version 9.4.) and RStudio software (R version 3.6.1). Prior to the analyses, the datasets were checked for outliers, which were excluded, if they were clearly miscalculations or typing errors. The datasets used in linear models were tested for normality (Shapiro–Wilk test) and homogeneity of variances (F-test). Generalized mixed models were done with GLIMMIX-procedure (response distribution normal, link function identity) in SAS and degrees of freedom were calculated using a Kenward–Roger correction. Tukey's HSD test was used for comparison of least squares means.

I inspected allometric growth of Harris mud crabs using Standardized Major Axis (SMA) regression models between carapace width and claw dimensions measured prior to the salinity experiment. Models were conducted with the *smart* package in R (v2.0; Falster et al., 2006). Males and females were compared in case there were differences in the level of allometry between sexes as shown in other studies (Mariappan et al. 2000). Allometric relations were described with equation $y = ax^b$ (Huxley, 1932), where y was claw dimension trait (CRH, CRL, CUH or CUL), x was CW and a and b were constants. This equation becomes linear after the logarithmic transformation, $\log_{10} y = b \times \log_{10} x + \log_{10} a$. Then the type of allometry can be determined from the slope b. Positive allometry ($b > 1$) indicates proportionally higher growth rate of studied trait (claw dimension) with increasing body size (CW), isometry ($b = 1$) means equal growth along body size and negative allometry ($b < 1$) means proportionally lower growth rate with increasing body size.

I created several generalized linear mixed models to test the effect of salinity on growth of moulted *R. harrisii* individuals. Because of the pronounced size-dimorphism, males and females were analysed separately. The first model tested the effect of salinity treatment on the growth rate of carapace width by using carapace width at the end of the experiment as the response variable and salinity, carapace width in the beginning of the experiment and their interaction as the predictors. The second model tested the effect of treatment on body weight by explaining body weight at the end of the experiment with treatment, body weight in the beginning of the experiment and their interaction. The other models examined the growth of claw dimensions (CRH, CRL, CUH, CUL) by explaining the claw growth (i.e. the difference of claw dimension after and before the experiment) with treatment, carapace width and their interaction. Each model described above included aquarium as a random factor.

I recorded survival as a binary variable: dead (0) or alive (1) at the end of the experiment. Likewise, moulting was considered as a binary variable: 0 for non-moulted and 1 for moulted individuals at the end of the experiment. I tested overall differences in survival and moulting between treatment groups and sexes with Fisher's exact test. I also calculated survival time and moulting time as days from the beginning of the experiment until the death and moult of the individual, respectively. Individuals, which did not moult but died during the experiment were considered as censored observations in the survival tests. I used the Kaplan-Meier method (Kaplan & Meier, 1958) to produce survival curves for visual comparison of survival and moulting rates between treatment groups and sexes. I conducted the Kaplan-Meier analysis and a pairwise comparisons (Log-rank test) with the *survival* (v2.38; Therneau, 2015) and the *survminer* (v0.4.6; Kassambara et al., 2019) packages in R. I computed survival and

moulting over time separately with multivariate Cox-Proportional hazard regression model and added treatment and sex as covariates, to evaluate their joint effects on survival and moulting.

I evaluated the relationship between the critical mussel size and morphological dimensions of mud crabs with several generalized linear mixed models (GLMM) in which critical mussel size was explained by crab body dimension (CW, CRH, CRL, CUH, CUL or BW), sex and their interaction. As crabs were randomly divided into separate aquaria, aquarium was added as a random factor into the models.

I used correlation analyses to evaluate connections between morphological dimensions of blue mussels. Also, the relationship between the force needed to break a shell and various morphological dimension was tested with regression analyses. I compared the mussel populations (Luvia and Tvärminne) for differences in shell strength when valve size was considered as a covariate (ANCOVA).

3. Results

3.1. Allometry of claws and carapace

All claw dimensions correlated linearly with CW in males and females (Table 1, Figure 3). The slopes of the regression lines varied in males between 1.265-1.351 and were thus significantly larger than 1 (Table 1), indicating positive allometry between carapace width and claw dimensions. The slopes in females varied between 1.033-1.104 and did not deviate significantly from 1 (Table 1), suggesting isometry between carapace width and claw dimensions. These slopes for CRL (X^2 (1) = 8.69, p = 0.003), CUH (X^2 (1) = 5.01, p = 0.025) and CUL (X^2 (1) = 5.01, p = 0.038) differed between sexes and even CRH was close to significance (X^2 (1) = 3.19, p = 0.074). These results suggest that large males invest proportionally more on claw size (except CRH) while female claws are proportionally equal sized in relation to carapace width. These differences in allometry between sexes underlie the sexual claw-size -dimorphism in *R. harrisii*.

Table 1. Allometric coefficients for relations of crusher height (CRH), crusher length (CRL), cutter height (CUH), cutter length (CUL) and carapace width (CW) of male and female *R. harrisii*. Results from regression

type II analyses (SMA) with log-transformed data. The sign + indicates positive allometry (b > 1) and 0 indicates isometry (b = 1). Log-log relationships and regression lines are shown in Figure 3.

Log Y - log X	Sex	n	a	b	r^2	Allometry	P
CRH - CW	Male	99	-0.766	1.351	0.961	+	<.0001
	Female	28	-0.571	1.104	0.701	0	0.364
CRL - CW	Male	100	-0.473	1.323	0.983	+	<.0001
	Female	28	-0.226	1.033	0.849	0	0.676
CUH - CW	Male	100	-0.851	1.328	0.973	+	<.0001
	Female	28	-0.594	1.033	0.709	0	0.762
CUL - CW	Male	99	-0.463	1.265	0.978	+	<.0001
	Female	27	-0.295	1.052	0.826	0	0.549

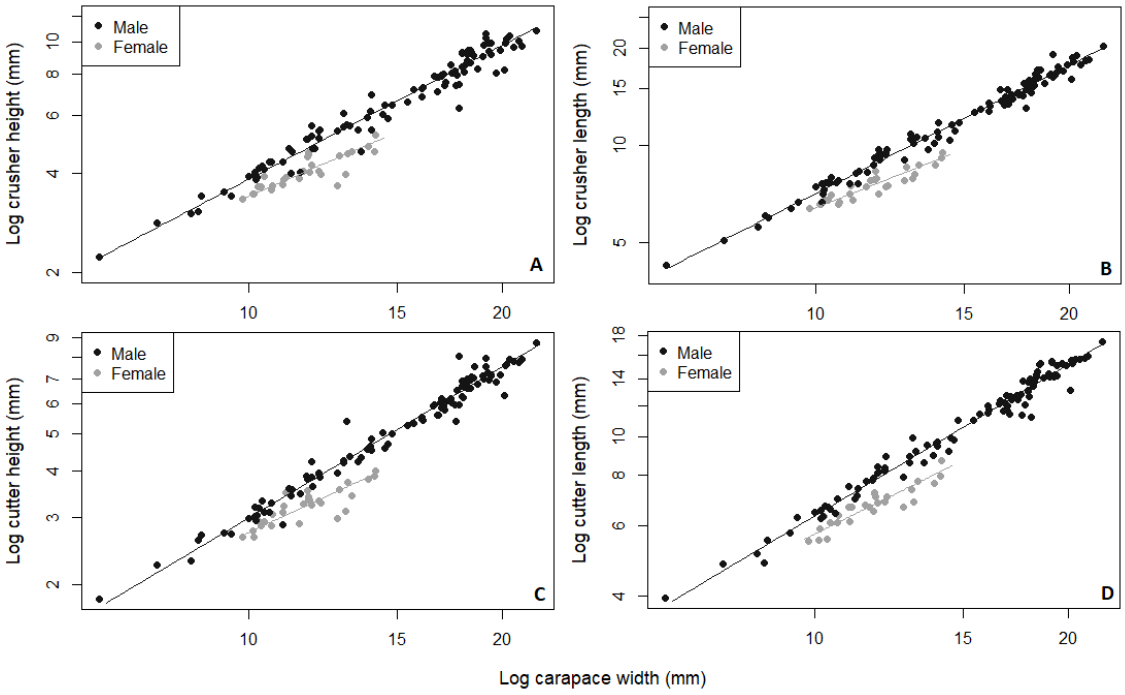

Figure 3. Log-log relationships between carapace width and crusher height (**A**), crusher length (**B**), cutter height (**C**) and cutter length (**D**). Intercepts and slopes of the regression lines presented in Table 1.

3.2. The effect of salinity on performance of Harris mud crabs

3.2.1. Growth

The growth of carapace width and body weight of *R. harrisii* did not differ between salinity levels of 2.5, 5.5 and 7.5 ppt, suggesting that salinity level does not affect the growth of carapace width or body weight (Table 2, Figure 4). There was a significant positive connection between pre-treatment and post-treatment carapace widths both in females and males (Table 2). The non-significant interaction between salinity level and pre-treatment carapace width

was excluded from the models (GLMM: males F(2, 37.43) = 1.33, p = 0.276; females F(2, 15) = 2.49, p = 0.117). Pre-treatment body weight influenced post-treatment body weight both in females and in males (Table 2). The non-significant interaction between salinity level and pre-treatment body weight (GLMM: males F(2, 24.46) = 2.84, p = 0.078; females F(2, 13) = 1.82, p = 0.201) was excluded from the models.

The growth of cutter claw height of male mud crabs was related to salinity level (Table 2). The growth was largest in treatment 7.5 and second largest in treatment 2.5 ppt (Figure 4). Growth of male CUH in treatment 7.5 ppt differed significantly from treatments 2.5 and 5.5 ppt (Tukey p = 0.03 and 0.004, respectively). Growth of other claw dimensions appeared to be unaffected by salinity level. The growth of claw dimensions of male mud crabs was significantly dependent on carapace width (Table 2) as claws of larger males grew more than claws of smaller males. The growth of claw dimensions of female mud crabs was not related to salinity level and, unlike in males, claw growth of female crabs did not differ between individuals of different CW (Table 2). The non-significant interaction of treatment and covariate carapace width was excluded from all the models.

Table 2. Results for the generalized linear mixed models predicting growth of the morphological dimensions with salinity treatment and pre-treatment carapace width or body weight. Males and females were analysed separately. Treatment consisted from three salinity conditions: 2.5, 5.5 and 7.5 ppt.

	Male			**Female**		
Response and explanatory variables	**df**	**F-value**	**P-value**	**df**	**F-value**	**P-value**
Carapace width[a]						
Treatment	2, 15.5	0.67	0.53	2, 8.69	0.66	0.54
Carapace width[b]	1, 34.9	3775	**<.0001**	1, 6.75	154	**<.0001**
Body weight[a]						
Treatment	2, 15.8	2.56	0.11	2, 15	0.05	0.95
Body weight[b]	1, 24.7	1064	**<.0001**	1, 15	84.9	**<.0001**
Crusher height growth						
Treatment	2, 11.8	2.18	0.16	2, 8.79	0.3	0.78
Carapace width[b]	1, 34.5	45.1	**<.0001**	1, 8.26	0.1	0.76
Crusher length growth						
Treatment	2, 15.6	1.65	0.22	2, 10.7	0.3	0.78
Carapace width[b]	1, 37.9	14.6	**<.001**	1, 5.53	0.9	0.39
Cutter height growth						
Treatment	2, 19.4	5.55	**0.012**	2, 17	1.4	0.28
Carapace width[b]	1, 36.9	14.4	**<.001**	1, 17	1.2	0.29
Cutter length growth						
Treatment	2, 18.6	1.35	0.28	2, 17	0.03	0.97
Carapace width[b]	1, 33.2	43.52	**<.0001**	1, 17	0.5	0.50

[a] Dimension measured after moulting. [b] Dimension measured before treatment (body size at start).

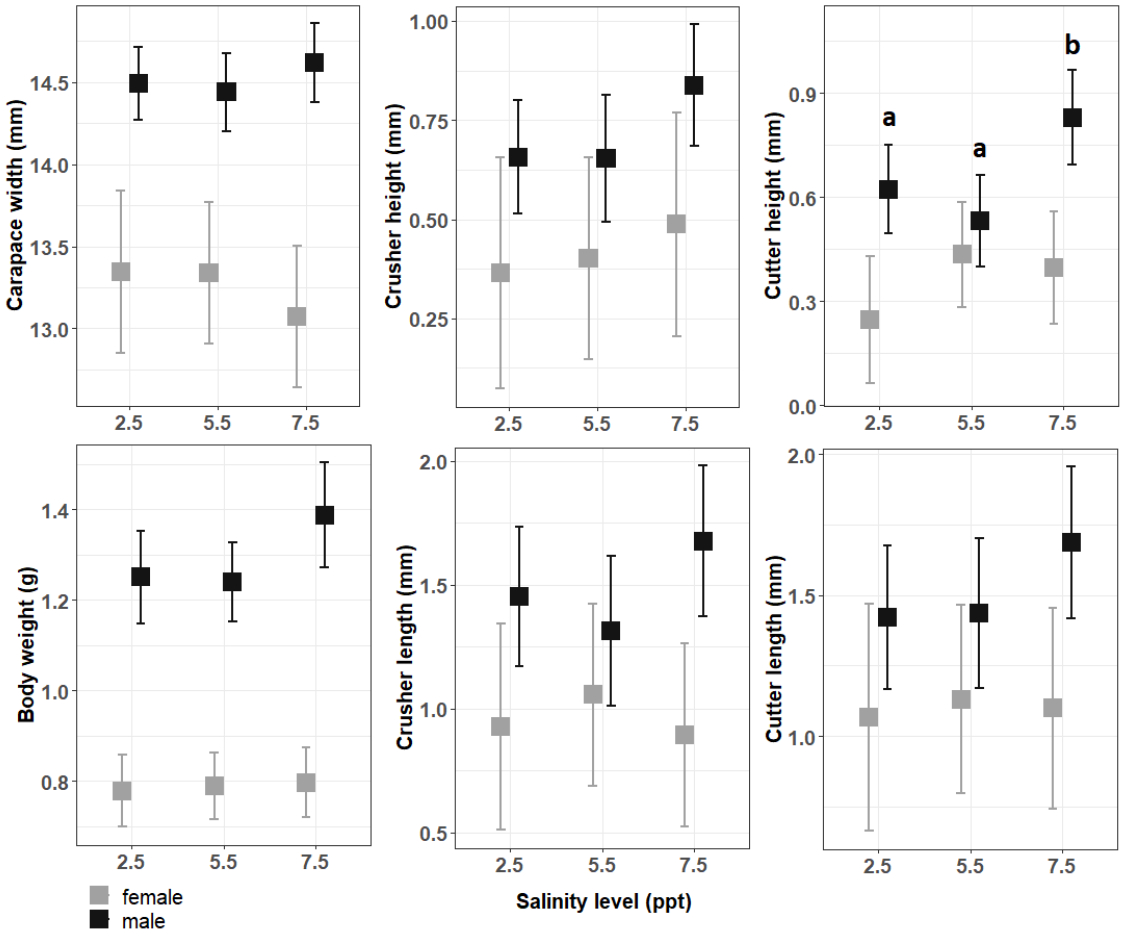

Figure 4. Least Squares (LS) means with ±95 % confidence intervals for the growth of carapace width, body weight, crusher claw height, crusher claw length, cutter claw height, cutter claw length of *R. harrisii* after 156 days exposure to the salinity levels of 2.5, 5.5 or 7.5 ppt. The number of observations was 23 males and 9 females in 2.5 ppt, 49 males and 9 females in 5.5 ppt, 30 males and 10 females in 5.7 ppt. Means with different letters are significantly different (cutter height, Tukey-adjusted comparisons).

3.2.2. Moulting

During the experiment 73 out of the 131 crabs moulted. Moulting probability of adult *R. harrisii* did not differ between the three salinity levels (Figure 5). Also, when joint effects of salinity and sex was analysed, salinity levels did not affect moulting probability (Wald X^2 (2) = 2.54, p = 0.28). Therefore, the result suggests that adult Harris mud crabs moult at the same rate in salinity range of 2.5-7.5, at least when the effects of salinity is monitored during one moult cycle.

There was a significant difference in moulting probability between female and male mud crabs during the experiment (Figure 6). Also, when joint effects of salinity and sex was analysed, sex influenced moulting probability significantly (Wald X^2 (1) = 5.63, p = 0.02). Females moulted

more likely than males with hazard ratio of 1.861 (95 % Cl 1.092-3.063). Fisher's exact test showed significant association between sex and moulting in salinity level of 5.5 ppt (Two-sided p = 0.026) in which 88.9 % of the females moulted while only 44 % of the males moulted. Most of the females moulted also in other salinity levels (2.5 ppt: 66.7 %, 7.5 ppt: 70 %). Most males in salinity 2.5 ppt moulted (73.9 %) while in treatments 5.5 and 7.5 ppt (43.3 %) the frequency of moulted males was slightly lower. Altogether, the results suggest that the overall moulting rate of adult Harris mud crabs is higher for females than males, especially in salinity of 5.5 ppt.

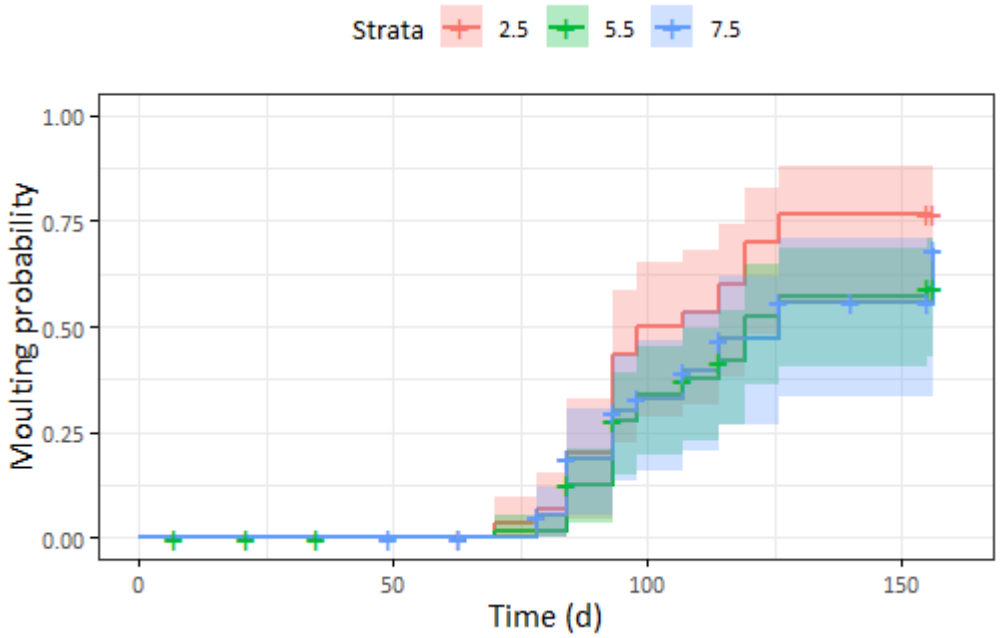

Figure 5. Moulting probability within treatment groups during the experiment. There were no significant differences in moulting probability between the three salinity treatments (Log-rank test X^2 (2) = 3.5, p = 0.2, 2.5 ppt n = 31, 5.5 ppt n = 58, 7.5 ppt n = 40). 95 % confidence intervals are indicated by shaded areas.

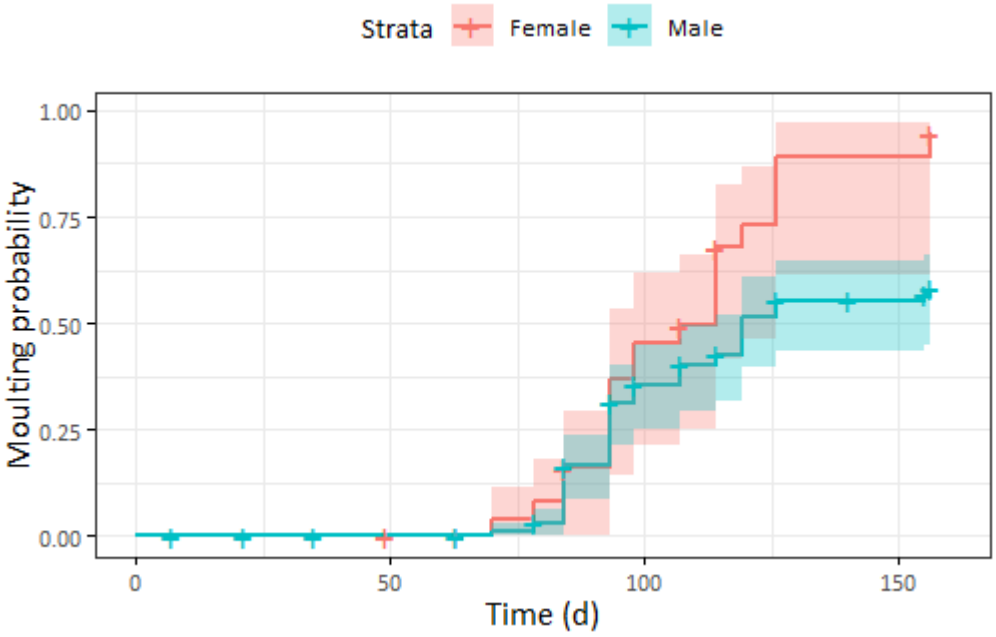

Figure 6. Moulting probability of the sexes during the experiment. Moulting probability of female mud crabs was higher than males' (Log-rank test X^2 (1) = 7.3, p = 0.007, male n = 102, female n = 27). Almost all females (95 %) had moulted at the end of the experiment. 95 % confidence intervals are indicated by shaded areas.

3.2.3. Survival

During the experiment 69 out of 131 crabs died. There was a significant difference in survival probability between salinity levels (Figure 7) also when joint effects with sex was considered (Wald X^2 (2) = 15.75, p < 0.001). The survival rate of the mud crabs did not differ between treatments 2.5 and 5.5 ppt (hazard ratio 0.971, 95 % CI 0.478-1.892), but compared to mud crabs in treatment 7.5 ppt, they died 0.374 (95 % CI 0.188-0.704) and 0.385 times (95 % CI 0.221-0.664) less likely, respectively. Increased mortality in salinity of 7.5 ppt suggests that mud crabs may undergo higher physiological costs in that salinity level than in the lower salinity levels.

There was no difference in survival probability between the sexes (Figure 8), either when joint effects with salinity levels were analysed (Wald X^2 (1) = 1.79, p = 0.18). There was no association between sex and overall survival in any of the treatment groups either (Two-sided Fisher's exact test; 2.5 ppt: p = 1.000, 5.5 ppt: p = 0.464, 7.5 ppt: p = 0.40). Mortality of the females was rather even in treatments 2.5 and 5.5 ppt (44.4 % and 55.6 %, respectively) while in salinity 7.5 ppt almost all females had died by the end of the experiment (90 %). Less than half of the males died in salinities 2.5 ppt and 5.5 ppt (43.5 % and 38 %, respectively) whereas in salinity 7.5 ppt 70 % of the males had died at the end of the experiment.

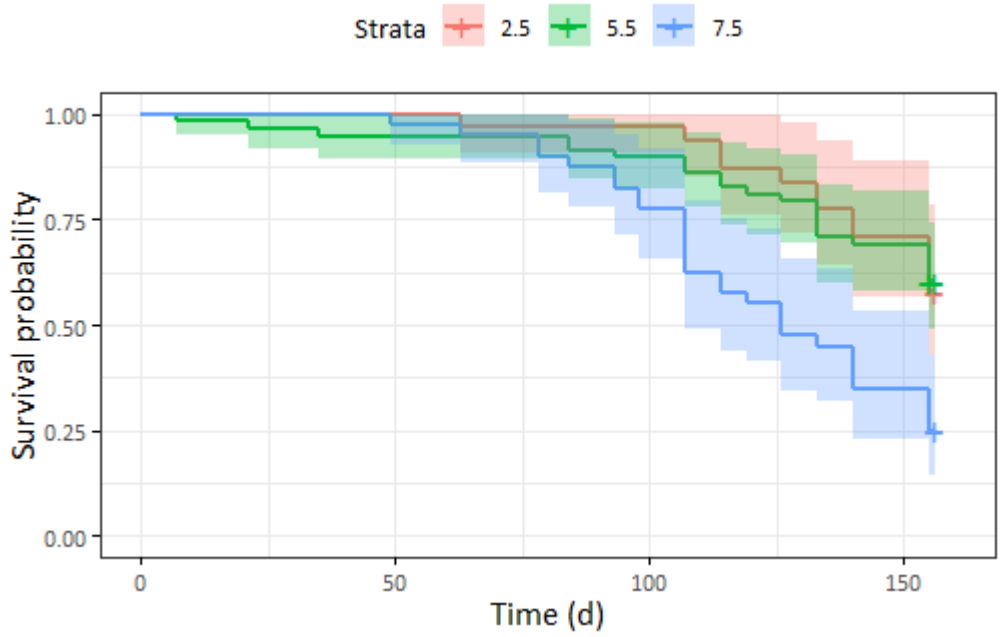

Figure 7. Survival probability within salinity levels during the experiment. Overall survival of mud crabs decreased most in 7.5 ppt compared to 2.5 and 5.5 ppt, which did not differ from one another (Log-rank test X^2 (2) = 17.6, p < 0.001, 2.5 ppt n = 31, 5.5 ppt n = 58, 7.5 ppt n = 40). 95 % confidence intervals are indicated by shaded areas.

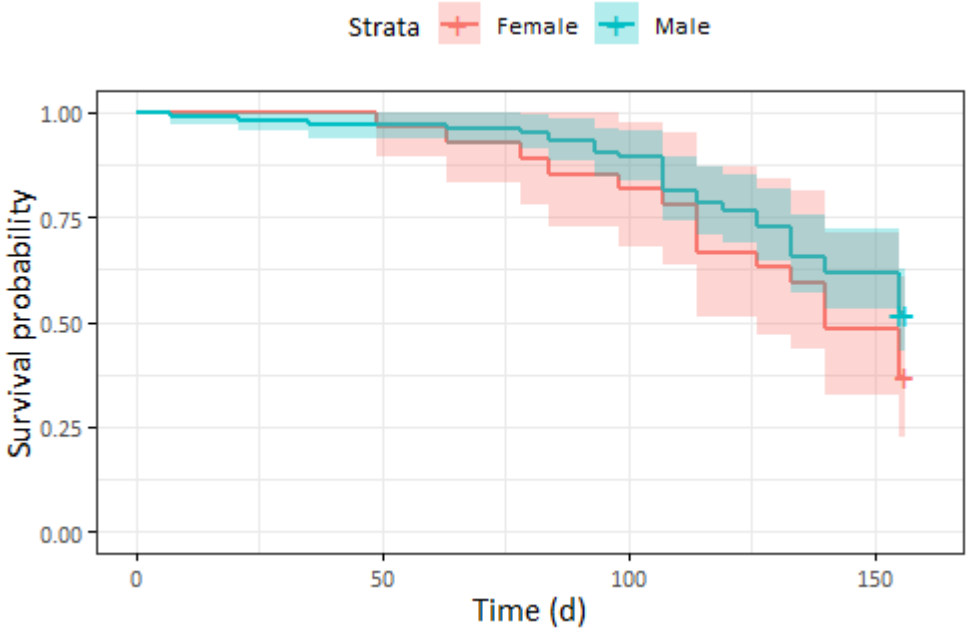

Figure 8. Survival probability within sexes during the experiment. There were no significant differences in survival probability between sexes (Log-rank test X^2 (1) = 2.1, p = 0.2, 2.5 ppt n = 31, 5.5 ppt n = 58, 7.5 ppt n = 40). 95 % confidence intervals are indicated by shaded areas.

To test whether salinity level had an effect on mortality after moulting, I used time between moult and death as the dependent variable, which I then compared between treatment groups with Kruskal-Wallis test. The number of days between moulting and death did not differ

between salinity levels (X^2 (2) = 0.613, p = 0.736). Therefore, it seems unlikely that salinity level influenced on how soon crabs died after moulting.

3.3. Critical size of blue mussels as a prey of Harris mud crabs

The critical length of the mussel increased with increasing carapace and claw size of the mud crab. Significant interaction term (sex × CW) indicated that CW affects critical length differently between sexes (GLMM: F(1, 72.12) = 11.14, p = 0.001), and therefore, I examined males and females separately. In both males and females, critical length increased with increasing CW (GLMM: males F(1, 52.63) = 120.01, p < 0.0001; females F(1, 17.98) = 11.13, p = 0.0037) but in males the increase was relatively higher in accordance with the differences in allometry (Figure 9). Also body weight (GLMM: F(1, 77.51) = 142.34, p < 0.0001) and sex (GLMM: F(1, 77.08) = 13.77, p = 0.0004) influenced significantly critical prey length, after the non-significant interaction was excluded (GLMM: F(1, 75.3) = 1.88, p = 0.174). Critical length increased with increasing BW but for males of a given weight critical length was larger (LS mean = 12.76, Cl 95 % 11.91-13.61) than for females (LS mean = 10.38, Cl 95 % 9.25-11.5).

The relation between claw dimensions and critical length showed clear differences between sexes depending whether claw height or length was considered. Crusher claw height had a clear positive effect on critical length (GLMM: F(1, 77.94) = 168.99, p < 0.001). The effect of sex was marginally non-significant (GLMM: F(1, 77.17) = 3.66, p = 0.059) (Figure 10), after the non-significant interaction between crusher claw height and sex was excluded from the model (GLMM: F(1, 73.94) = 1.69, p = 0.197). As the effect of sex was marginally non-significant, it could imply that critical length was slightly larger for male crabs (LS mean = 12.35, Cl 95 % 11.46-13.24) than female crabs (LS mean = 11.15, Cl 95 % 10.02-12.29) in relation to CRH. Cutter claw height responded similarly than CRH with positive effect on critical length (GLMM: F(1, 73.17) = 156.10, p < 0.0001). Also sex explained critical length (GLMM: F(1, 77.18) = 5.11, p = 0.027), after the non-significant interaction was excluded (GLMM: F(1, 74.83) = 2.50, p = 0.118). Critical length was larger for males (LS mean = 12.49, Cl 95 % 11.65-13.34) than for females (LS mean = 11.02, Cl 95 % 9.88-12.17) of a given CUH. Altogether, the results show that critical length did differ between males and females of equal claw height, as males could crush larger mussels in relation to claw height.

On the other hand, critical length did not differ between males and females of equal claw length. Crusher claw length did influence critical length (GLMM: F(1, 76.58) = 152.46, p < 0.0001) (Figure 11) but sex (GLMM: F(1, 72.97) = 1.14, p = 0.289) and their interaction (GLMM:

F(1, 74.24) = 3.09, p = 0.083) did not. Also cutter claw length did influence critical length (GLMM: F(1, 75.16) = 41.62, p < 0.0001) while sex (GLMM: F(1, 71.93) = 1.23, p = 0.272) and their interaction (GLMM: F(1, 73.36) = 3.34, p = 0.072) did not. Critical length increased with increasing CRL and CUL.

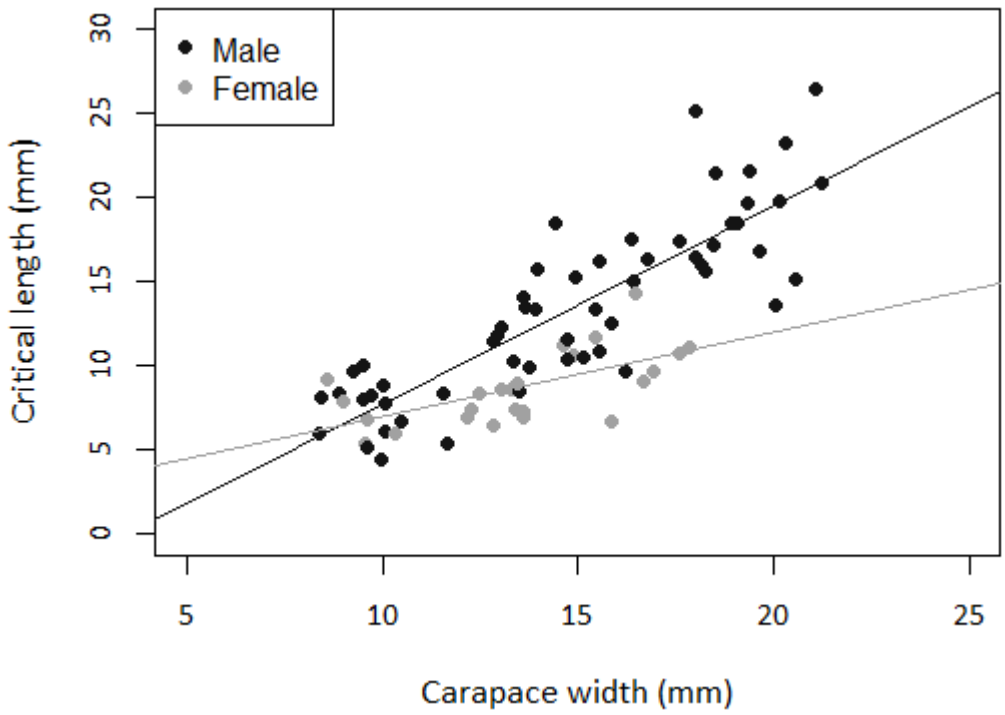

Figure 9. Regressions of critical length of blue mussels and carapace width of male and female mud crabs. Critical length presents the mean length of largest eaten and smallest non-eaten mussel of a given crab individual. Males: critical length = -4.036 + 1.18CW, r^2-adj. = 0.723, p < 0.001, and females: critical length = 2.027 + 0.499CW, r^2 = 0.35, p < 0.001.

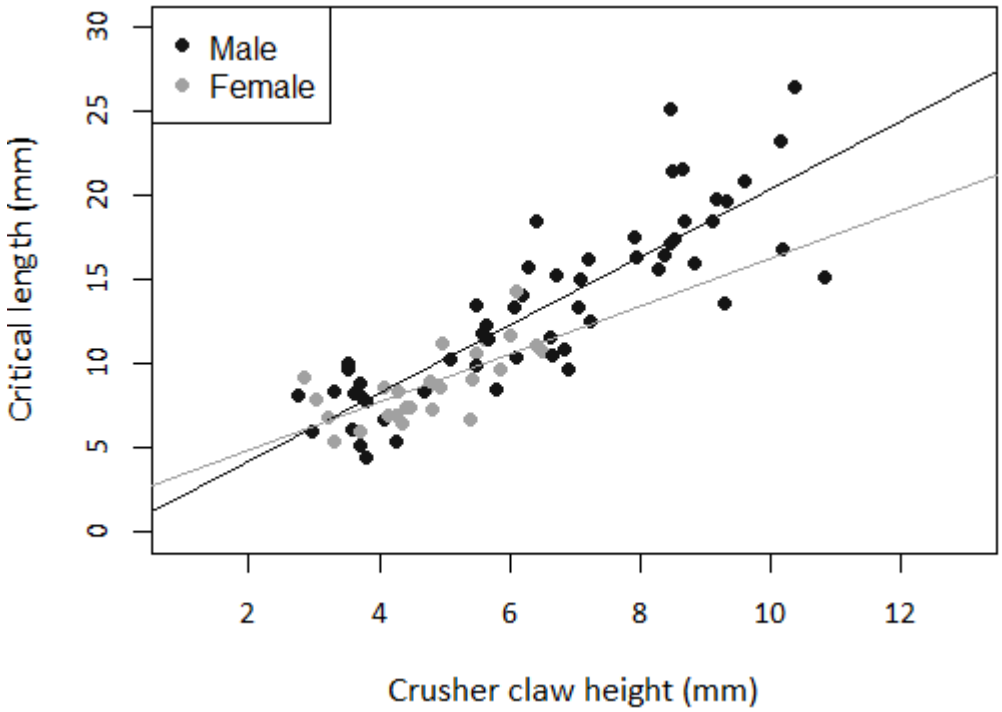

Figure 10. Regressions of critical length of blue mussels and crusher claw height of male and female mud crabs. Critical length presents the mean length of largest eaten and smallest non-eaten mussel of a given crab individual. Males: critical length = 0.181 + 2.02CRH, r^2-adj. = 0.729, $p < 0.001$, and females: critical length = 2.001 + 1.428CRH, $r^2 = 0.46$, $p < 0.001$.

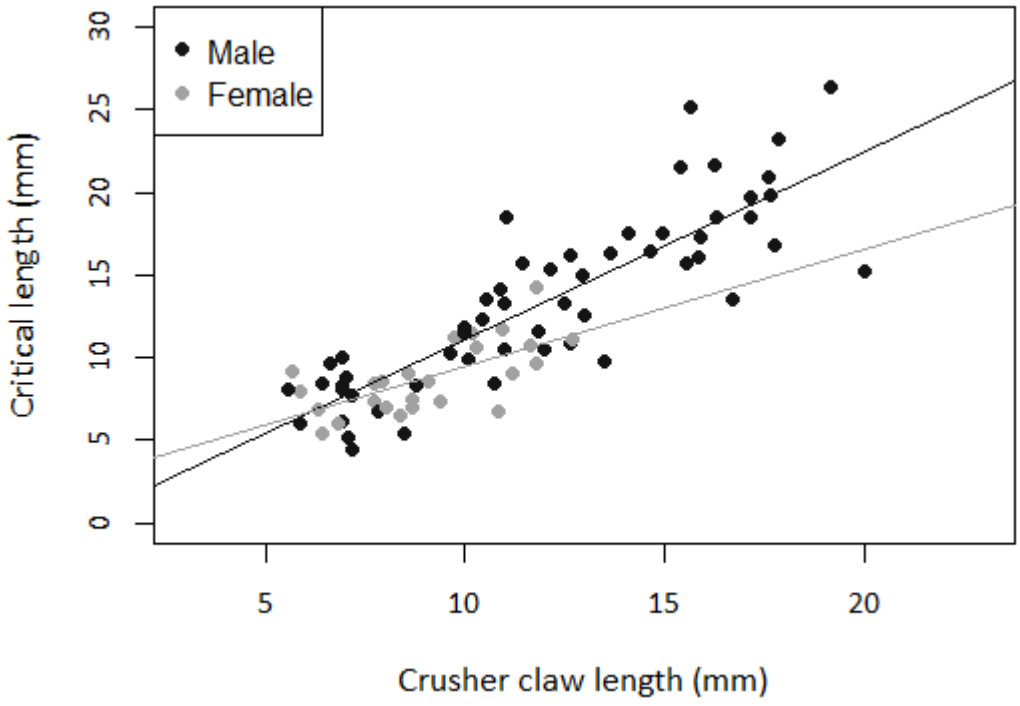

Figure 11. Regressions of critical length of blue mussels and crusher claw length of male and female mud crabs. Critical length presents the mean length of largest eaten and smallest non-eaten mussel of a given crab individual. Males: critical length = -0.175 + 1.132CRL, r^2-adj. = 0.718, $p < 0.001$, and females: critical length = 2.396 + 0.705CRL, $r^2 = 0.409$, $p < 0.001$.

3.4. Morphometries and shell strength of blue mussels

There were strong positive correlations between width, length, height and weight of blue mussels (Pearson correlation r > 0.90). These dimensions also correlated positively with valve strength (width r = 0.53, length r = 0.50, height r = 0.54 and weight r = 0.56) indicating that valve strength increases with increasing size of the shell.

Table 3. Range and mean values with standard errors of the morphological dimension and valve strength of blue mussels from populations of Luvia and Tvärminne. Strength is calculated as a mean of the forces (N) needed to break right and left valve.

Population	n	Dimension	Mean ± SE	Range
Luvia	46	Length	24.11 ± 0.73	15.27 - 33.58
		Width	12.86 ± 0.37	8.83 - 17.95
		Height	10.47 ± 0.33	7.05 - 15.8
		Weight	1.68 ± 0.15	0.47 - 4.29
		Strength	19.19 ± 1.25	3.3 - 40.0
Tvärminne	36	Length	15.85 ± 0.75	8.21 - 23.89
		Width	8.83 ± 0.37	5.12 - 13.68
		Height	6.78 ± 0.33	3.48 - 11.51
		Weight	0.54 ± 0.07	0.08 - 1.88
		Strength	16.33 ± 1.05	7.53 - 30.53

Mussels were sampled from two areas, which differed in salinity (surface salinity 4 ppt in Luvia and 5.07 ppt in Tvärminne (Finnish Environment Institute, 2020)) and these populations were compared for differences in morphometrics and valve strength. Mussels from Luvia were significantly longer (ANOVA $F(1, 80) = 61.35$, $p < 0.0001$), wider (ANOVA $F(1, 80) = 58.36$, $p < 0.0001$), higher (ANOVA $F(1, 80) = 59.69$, $p < 0.0001$) and heavier (ANOVA $F(1, 80) = 40.36$, $p < 0.0001$) than mussels from Tvärminne (Table 3). There was a significant influence of population on valve strength (ANCOVA: $F(1, 79) = 4.21$, $p = 0.04$) when size was kept constant by including valve length as a covariate (Figure 12). Valve length was positively related to valve strength (ANCOVA: $F(1, 79) = 21.32$, $p < 0.0001$). I excluded the non-significant interaction of population and valve length (ANCOVA: $F(1, 78) = 0.01$, $p = 0.92$). As could be expected based on the difference in salinity, results indicate that mussels of a given length had stronger shells in Tvärminne than in Luvia (LS means strength: Tvärminne 20.16 N, Cl 95 % 17.56-22.76; Luvia 16.19 N, Cl 95 % 13.97-18.41).

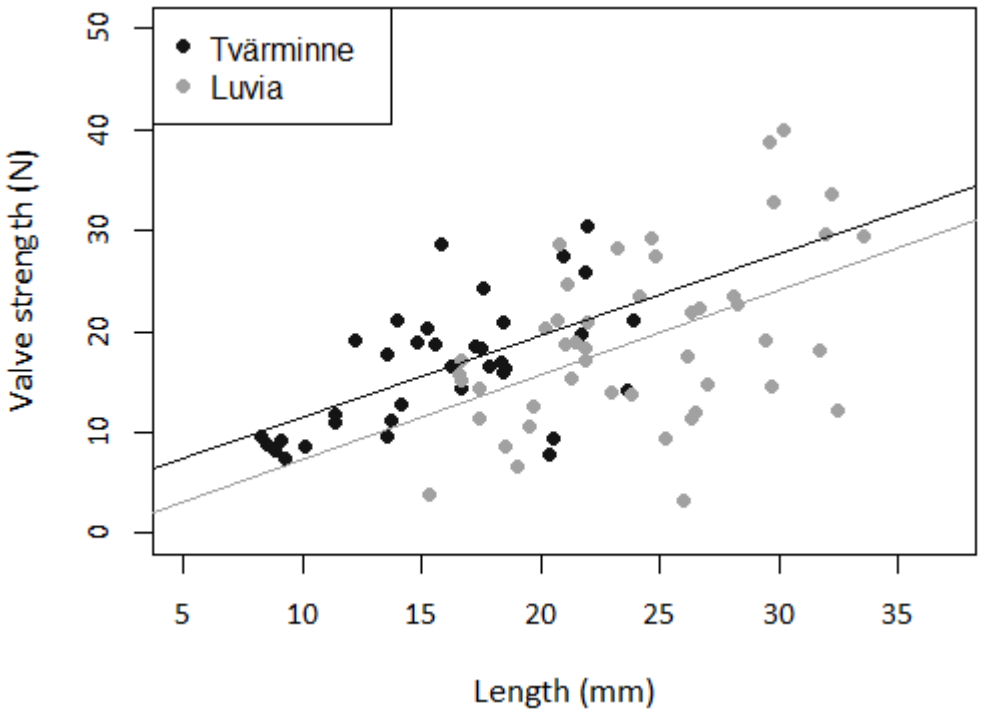

Figure 12. Regressions of valve strength and length of blue mussels from two populations. Tvärminne: strength = 3.583 + 0.807length, r^2-adj. = 0.313, $p < 0.001$, Luvia: strength = -1.077 + 0.841length, r^2 = 0.222, $p < 0.001$.

4. Discussion

In this thesis, I have focused on the effects of environmental change, particularly salinity, on a novel, invasive predator, Harris mud crab (*Rhithropanopeus harrisii*) and its interaction with a native prey, blue mussel (*Mytilus trossulus*). With an experimental approach I assessed how salinity influences the ecology of the Harris mud crab through alterations in survival and growth of claws and body size. For the first time, the effects of salinity on growth and survival of adult *R. harrisii* were studied. Also, this was the first time the critical size of the Baltic Sea mussels as a prey for non-native *R. harrisii* was determined. I found that the growth of Harris mud crabs is hardly affected by the salinity gradient of the Baltic Sea and that there is a clear relationship between the critical size of the mussel and the claw and body size of the mud crab. It seems that there are only minor effects on growth and claw allometry of the Harris mud crab that could affect the critical prey size and, therefore, change the ecological impact of the predator on mussel populations. Instead, decreasing salinity in the future may influence the predation-prey interaction via alteration in mussel size. Survival of the mud crabs increased in lower salinity levels suggesting that Harris mud crabs of the Archipelago Sea are well-adapted to low salinities.

4.1. Allometry of claws and carapace

Comparison of allometry of claw growth in relation to carapace width showed that males had positive allometric claw growth with increasing body size, whereas females had isometric claw growth. Hegele-Drywa and others (2014) reported similar results regarding the allometry of male crusher length, but in contrast to my findings, also a positive allometry of female crusher length. The difference in results may be explained by the larger sample size (female n = 269, male n = 283) or larger body size range (CW range of females 4.41–19.41 mm, mean 10.17 ± 3.15 mm, n = 370 and males 4.41–21.40 mm, mean 9.90 ± 3.97 mm, n = 400) in their study. However, it is worth to notice that, in general, that claw allometry differs between sexes in those decapod species, which have sexually dimorphic claws. Often males show positive allometry and females show either isometric or negative allometry (Mariappan et al., 2000). There is stronger selection for large claws in males as they are beneficial during mate competition and interspecific agonistic interactions (Stein, 1976; Lee & Seed, 1992). Therefore, males allocate more resources on claw growth than females, especially during reproduction season (Heuring & Hughes, 2019).

The number of males was higher than females in all samples when the crabs were caught, and this resulted in a biased number of males and females in the experiments. Biased sex ratio towards males is common in crab populations, including the Harris mud crab and other species from the Xanthidae family (Helege-Drywa et al., 2014). Male-biased sex ratio has been reported in the populations of the Baltic Sea as well as in the native populations in North America (Ryan, 1956; Turoboyski, 1973; Hegele-Drywa et al., 2014). As Helege-Drywa and others (2014) point out, varying sampling gear and sampling season between studies could affect the size and sex ratio of the sampled mud crabs, because season is closely linked with reproduction or moulting period and foraging behaviour. Sampling method in the present study required active movement of mud crabs, that could indeed differ between sexes. However, as the Helege-Drywa and others (2014) further discuss, differences in carapace dimensions or sex ratio have occurred also in other crab species inhabiting distant locations.

4.2. Salinity affects the performance of the Harris mud crab

Salinity experiment showed that the growth of body size of *R. harrisii* did not differ between salinity levels of 2.5, 5.5 and 7.5 ppt. Therefore, it seems that the salinity gradient of the Baltic

Sea does not cause difference in the body size of adult mud crabs in the Baltic Sea. Likewise, future decrease in salinity within salinity range of 2.5-7.5 ppt would not affect the growth of body size. Also, most of the claw dimensions were not affected by salinity except the growth of cutter claw height of male *R. harrisii*, that increased significantly from 5.5 to 7.5 ppt. This suggests that salinity has the potential to affect the growth of claws. The growth of other claw dimensions in male crabs showed slight tendency of increase in salinity level 7.5 ppt compared to 2.5 and 5.5 ppt, but all in all, there was no statistically significant difference in the growth of these dimensions. Females did not show any variation in growth among salinity levels. Growth increment of carapace width and body weight in female mud crabs was clearly less than in male mud crabs. The growth difference in weight relates to sexual dimorphism of claws, as male mud crabs gain more weight due to enhanced growth of claws. Also, male carapace width seemed to increase more during a moult cycle, which explains the larger body size of males compared to females. In addition to growth increment also moulting rate influences the overall growth rate of the mud crabs (McLay, 2015). Salinity did not affect moulting rate, which further suggests that the growth rate of mud crabs does not vary in the salinity range of the Baltic Sea. It is worth to notice that the effects of salinity were studied only with adult specimens and within limited time period, so these results may not apply for juveniles or in case of long-term exposure to salinities in question.

Interestingly, the survival probability was significantly smaller in the salinity of 7.5 ppt than in the two lower salinity levels. Both males and females responded similarly. Increasing survival with decreasing salinity suggests that adult Harris mud crabs of the Archipelago Sea are well adapted to tolerate low salinities. The population of the Archipelago Sea may have adapted to local conditions during the establishment or the founding individuals may have originated from an estuarine population of high tolerance to low salinities. Changes in survival due to variation in salinity could affect the population growth and influence population densities along the salinity gradient. It would mean higher densities of adult individuals when salinity falls under 7.5 ppt. In the future, survival might increase among *R. harrisii* populations of the southern Baltic Sea with decreasing salinities if they origin from the same source population than the studied population, and thus share similar tolerance to low salinities. This would also require that the population of Archipelago Sea had not adapted to low salinity conditions after the establishment. As there is genetic divergence between Baltic populations of *R. harrisii* (Forsström et al., 2017), the results of the present study cannot be directly generalized to other Baltic populations because their tolerance to salinity conditions may differ.

It is unlikely that the further invasion of adult Harris mud crabs from the Archipelago Sea to the northern and eastern gulfs of the Baltic Sea is hindered by the decreasing salinity because

survival and the growth of claws and body size of mud crabs did not differ between salinities of 5.5 and 2.5 ppt. Despite the apparent tolerance of adult individuals to low salinities, it is unknown whether Harris mud crabs could reproduce in salinity of 2.5 ppt. Adult individuals and breeding populations have been found even in freshwater habitats (Boyle et al., 2010). However, *R. harrisii* populations differ in minimum salinity for hatching and larval development ranging from 0.5 to 5 ppt (Costlow et al., 1966; Laughlin & French, 1989; Boyle et al., 2010). Reduced reproduction success in the northernmost Baltic Sea could be expected if larval hatching requires salinities above 5 ppt (Costlow et al., 1966; Holopainen et al., 2016) but the population of the Archipelago Sea could also be well adapted to reproduce under 5 ppt. In the present study, higher mortality in salinity of 7.5 ppt could support the latter, but further studies on minimum required salinity for reproduction would be needed.

Salinity in the Baltic Sea is predicted to decrease in the future due to climate change. In the light of the present study, Harris mud crabs, which originally inhabited salinities of 7.5 ppt would experience a decrease in the growth of male cutter claws. If salinity in the current distribution range of *R. harrisii* in the Archipelago Sea decreased to 2.5 ppt, the direct consequences on the growth and survival of adult mud crabs would be negligible. Salinity in the northeastern gulfs of the Baltic Sea could eventually approach zero. Other studies show that adult Harris mud crabs survive well in freshwater (Boyle et al., 2010), but the effects of salinities below 2.5 ppt on growth and survival were not considered in the present study.

It is a worth to notice that in addition to decreasing salinity, other abiotic factors will determine the development of mud crab invasion in the future. One factor is rising temperatures due to climate change that could, in fact, enhance the reproduction and growth of *R. harrisii* in the Baltic Sea (Hegele-Drywa & Normant, 2014; Turoboyski, 1973). However, further consideration of interacting effects of salinity and other abiotic factors on invasion of *R. harrisii* is beyond the scope of this study.

4.3. Critical size of blue mussels as a prey of Harris mud crabs

The critical prey size was proportional to the size of a given Harris mud crab individual. Increasing body size allowed mud crabs to consume larger prey than what their smaller counterparts were able to consume. Critical mussel length for an average-sized Harris mud crab (CW 14.42 mm) was 11.98 mm. Comparisons of carapace width and critical mussel length showed that male and female mud crabs with the same carapace size have different capacity to handle hard-shelled prey. Critical mussel length for an average-sized male mud crab (CW

14.84 mm) was 13.47 mm while for an average-sized female (CW 13.52 mm) it was 8.77 mm. Mussels reach a size refugia sooner from female mud crabs than from male mud crabs; largest observed critical mussel length for males was 26.43 mm and for females 14.31 mm in length. As the results on allometric growth showed, male claws grow at a faster rate than female claws do and therefore males of a given carapace width are capable to handle larger prey than females of the same carapace width. From carapace width of 8.5 mm critical length increases more steeply for males than females of a given size. Critical length overlaps in 5.99 mm for the smallest males and females of 8.5 mm in carapace width.

I found strong positive relationship between all claw dimensions and critical prey length. Especially crusher claw height is linked to claw strength and prey size selection in crabs (Lee & Seed, 1992; Lee, 1993; Behrens Yamada & Boulding, 1998; Schenk & Wainwright, 2001), that makes it a fundamental dimension when critical prey size is assessed. Average-sized crusher claw height in males was 6.57 mm and in females 4.74 mm, which related to critical lengths of 13.47 mm and 8.77 mm, respectively. The results suggest that male mud crabs could crush larger mussels than females with equal-sized crusher height. A same but clearer difference was also detected with cutter claw height. This would indicate that male claws of a given height are more capable of handling hard-shelled prey than female claws. Therefore, claw height may not fully correspond to claw strength and prey handling capacity but rather there are other claw properties that impact positively on critical mussel size of male crabs.

Claw length could be more suitable predictor for critical blue mussel length of *R. harrisii*. The relation of claw length and critical mussel length showed that males and females of a given crusher or cutter length could crush equal-sized blue mussels. Critical mussel length for average-sized male crusher length (12.05 mm) was 13.47 mm while for average-sizes female crusher length (9.04 mm) it was 8.77 mm. The results suggest that the difference in maximum prey size between sexes may be mainly related to differing allometry of carapace size and claw length. Also Milke and Kennedy (2001) concluded that claw length (and gape) of *R. harrisii* is likely a limiting factor for opening bivalve prey instead of crushing force. When they examined mechanical advantage (i.e. a ratio of specific claw dimensions that demonstrates crushing force and speed) of the claws of *R. harrisii*, they found out that it did not change with carapace size and there was no difference in crusher or cutter claws between males and females. This indicates that crushing force is constant despite claw size or sex, and thus differences in prey handling capacity of *R. harrisii* are not related to crushing force.

The present study is the first to examine the critical size of the Baltic blue mussels as a prey of non-native *R. harrisii* and, altogether, very few studies have been conducted on critical prey size of *R. harrisii*. Milke and Kennedy (2001) examined critical length of the hooked mussel

Ischadium recurvum and the dark falsemussel *Mytilopsis leucophaeata* as a prey of *R. harrisii* in Chesapeake Bay. According to their results, for a mud crab individual of 14.42 in carapace width (i.e. average-sized individual in the present study) critical length of *I. recurwum* was 11.26 and *M. leucophaeata* was 15.62 mm. Therefore, average critical length of blue mussel (11.98 mm) is close to critical length of *I. recurwum*. Largest observed critical length of *I. recurwum* was 16.2 mm, while there was no refuge in size for individuals of *M. leucophaeata,* because the largest specimen (26.7 mm) found was eaten by a 15.5 mm (CW) individual of *R. harrisii*. In the present study, largest observed critical blue mussel length was 26.43 mm eaten by an individual mud crab of 21.08 mm in carapace size. It is worth to notice that Milke and Kennedy changed each mussel after 3-d period and they represented critical size as largest mussel size that could be open, while in my thesis each mussel was kept for 24-h with fasting periods in between and critical size was calculated as the average between the largest opened mussel and the smallest unopened mussel.

Prey size selection in crabs is influenced by the size relationship between crab and prey, degree of satiation, claw gape, claw strength, dentition and total prey-handling time (Behrens Yamada & Boulding, 1998). Preference for prey well below the critical size is common characteristics for crab species and may be a result of passive mechanical selection (Lawton & Hughes, 1985) or active choice in order to maximize energy intake, minimize prey-handling time or avoid claw damage (Hughes & Seed, 1981; Juanes, 1992; Seed & Hughes, 1995). Forsström and others (2015) showed that also *R. harrisii* of a wide size range (mean carapace width ± SD = 16.74 ± 2.49 mm, range 10.8–19.95 mm) preferred small (5-10 mm) and medium (12-15 mm) sized blue mussels. In the present study, upper blue mussel size limit for female mud crabs was under 15 mm while for 42.9 % of the males it exceeded 15 mm. In accordance with optimal foraging models (reviewed by Schoener, 1971; Pyke et al., 1977; Krebs, 1978), preference for smaller mussels could be related to their high profitability when handling time or effort and gained energy is considered. As male Harris mud crabs have greater potential to prey on mussels of wider size range, their predatory activities may have larger impact on blue mussel population structure. Therefore, sex ratio of the mud crab population could impact the size-selective predation pressure. If sex ratio is male-biased, there could be more large mud crabs and therefore predatory impact on wider size range of blue mussels.

The present experiment also showed that *R. harrisii* can increase mussel mortality indirectly by damaging the valves lethally but leaving the mussel unconsumed. Some mud crab individuals consumed the whole mussel while others seemed to crush only parts of the valve and left the mussel otherwise intact. Same behaviour during a prey selection experiment was reported by Milke and Kennedy (2001).

4.4. Blue mussels in low saline areas of the Baltic Sea are more vulnerable to mud crab predation

As expected, shell strength increased with body dimensions of blue mussels. For predator mud crabs, increasing shell strength with increasing body dimensions of blue mussels means harder shelled prey with increasing prey size. Comparison of the mussel populations showed that mussels from Tvärminne had stronger shells in relation to length of the shell. Spatial variation in shell strength can result from differences in environmental conditions, such as salinity level (Nagarajan et al., 2006). Surface salinity in Luvia and Tvärminne differed from 4 ppt to 5.07 ppt, respectively. Westerbom and others (2002) showed that a salinity change from 6.5 to 5 ppt was enough to cause substantial decline in mean mussel size in the north-eastern Baltic Sea. Although two samples are not enough to demonstrate the effects of salinity on the difference in shell strength between Tvärminne and Luvia, salinity is a very likely factor contributing to this difference.

Because shell strength in relation to shell length can differ between blue mussel populations, the effort that mud crabs need to crush a certain sized mussel shell may vary between different locations. If shell strength decreases with decreasing salinity, it would also mean decreasing crushing effort, and thus increasing critical mussel size towards areas of lower salinities. The force needed to crush a mussel from Luvia was approximately 4 N less than the needed force for crushing an equal-sized mussel from Tvärminne. A crushing force of 4 N equated 4.97 mm in mussel length. Put quite simply, it means that a Luvia mussel crushed by a mud crab would be 4.97 mm larger in length compared to a stronger Tvärminne mussel crushed by the same crab with equal force. As critical length would increase with decreasing salinity, Harris mud crabs in the northern Baltic Sea could prey on relatively larger mussels compared to their southern conspecifics. In addition, predicted decrease in salinity due to climate change might cause overall decrease of shell size and strength in blue mussels, which would become more vulnerable to crab predation.

Small sized mussels are most vulnerable to predation as they are more preferred by mud crabs and available for wider size range of mud crabs. Vuorinen and others (2002) described abundance, biomass, size distribution and growth of the blue mussel along a transect from inner to outer archipelago. Abundance and biomass increased from inner to outer archipelago. Maximum size of mussels was under 40 mm, with a large part of the population being smaller than 20 mm in length, which was compatible with similar observations from the eastern and central Baltic Sea areas. Blue mussels of 15 mm or less in shell length had highest densities

along the sampled transect. Optimal growth conditions were found in the middle archipelago whilst growth decreased both towards (lower salinity) and away from the mainland (lower temperature and chlorophyll content). As large part of the mussel population is under 20 mm in length, they fall below the largest observed critical length (26.43 mm) presented in this study. Therefore, a large part of the blue mussel population in the Archipelago Sea could be under predation pressure by the largest mud crab individuals. However, the average critical mussel length of studied mud crab population was 11.98 mm, so predation pressure focuses on smaller and most abundant blue mussels. Westerbom and others (2002) showed that blue mussels over 20 mm are absent in the Gulf of Finland altogether due to salinities less than 6 ppt. In salinity of 5 ppt, maximum attainable size of mussels falls close to 10 mm. For these mussels, there would not be a size refugia from predation by the largest crabs, if Harris mud crabs invaded further to the Gulf of Finland. Also, overall abundances of mussels would further decrease with decreasing salinity in the future. It is likely, that in salinities less than 6 ppt, blue mussels are especially vulnerable to the effects of predatory activities of the Harris mud crabs.

5. Concluding remarks and future perspectives

As this thesis shows, the growth of the adult Harris mud crab is, for the most part, not affected by variation in salinity levels of the Baltic Sea. Therefore, it is unlikely that the adult Harris mud crabs of the current Baltic population go through substantial changes in growth related to the present salinity gradient and predicted decrease of salinity in the future. The Harris mud crab population collected from the Archipelago Sea is well-adapted to low-salinity conditions that might explain increased mortality in salinity of 7.5 ppt. Adult mud crabs have potential to invade further to the low saline northern and eastern gulfs of the Baltic Sea without alterations in growth of claw and body size. Larvae and juveniles may be more susceptible to variation in salinity. Unaltered growth of adult mud crabs would also suggest that the size-selective predation on blue mussel populations would not change in decreasing salinity conditions, at least down to 5.5 and 2.5 ppt in which the growth of male cutter claw height was lower than in salinity of 7.5 ppt. Decrease in cutter claw height with decreasing salinity may not alter the size-selective predation because the crusher claw size plays greater role in prey selection (Elner, 1980) and the size of blue mussels decreases as well. All in all, my thesis implies that the effects of salinity on the predator-prey interaction between the Harris mud crab and the blue mussel occur mainly via changing mussel size and shell strength and less via altered growth and survival of *R. harrisii*.

This thesis confirms that *R. harrisii* is well-adapted to low saline environments such as the Baltic Sea. Its capability to allocate energy between osmoregulation and other physiological functions may ensure stable growth in salinity range of 2.5-7.5 ppt. Whether this range contains the optimal salinity for the Harris mud crab of the Archipelago Sea is unknown as further experiments along wider salinity range would be needed to determine optimal salinity for growth of *R. harrisii*.

Crabs can have a substantial effect on bivalve populations (Seed, 1993). This thesis shows that *R. harrisii* has the potential to prey on blue mussels of rather wide size range. Predation of *R. harrisii* is limited by the size relationship between the mud crab and the blue mussel. The difference in maximum prey size between mud crab males and females is rather related to differing allometry of carapace size and claw length than to differing crushing capacity of male and female claws. Large mussels can reach a size-refugia from crab predation altogether. However, the proportion of mussel population, which is susceptible to crab predation increases with decreasing salinity. A large part of the blue mussels in the Archipelago Sea are smaller than the size required for refugia presented in this study. Moreover, the mean size of mussels decreases towards the low saline northern and eastern bays of the Baltic Sea and mussels may not reach size refugia from potentially invading Harris mud crabs in salinities less than 6 ppt.

In the future, blue mussels are expected to be negatively affected by the decreasing salinities due to climate change. The growth of blue mussels may decrease, abundance of large individuals diminishes and eventually the range margin could withdraw from areas with salinity level under 4 ppt (Westerbom et al., 2002; Vuorinen et al., 2015). Slower growth rate of blue mussels would expose them to mud crab predation for longer time period or prevent them from reaching the size-refugia altogether. For crabs, they would be more available source of food especially when small individuals in mussel patches would otherwise be sheltered by larger mussels, which might have reached the size refugia.

When the impact of mud crab predation on blue mussel populations in the Baltic Sea is evaluated, it is worth to notice that the proportion of bivalves in natural diet of Harris mud crabs is largely unknown. Also, various factors, such as predation by fishes, may regulate abundance and size-structure of the population of *R. harrisii* and directly alter predation pressure on local blue mussel populations. Therefore, further research would be needed to quantify the predatory impact of *R. harrisii* in natural blue mussel populations and whether there are spatial differences in predation risk depending on population structure of the Harris mud crab.

6. Acknowledgements

I want to thank my supervisors Veijo Jormalainen and Sami Merilaita for their support and guidance, which made this thesis possible. I thank Jenni Kauppi and Päivi Kotitalo for their assistance in setting up the salinity experiment. Also, I want to thank Archipelago Research Institute of the University of Turku for the facilities and Finnish Marine Research Infrastructure (FINMARI) for providing the infrastructure.

7. References

Aronhime, B. R., & Brown, K. M. (2009). The roles of profit and claw strength in determining mussel size selection by crabs. *Journal of Experimental Marine Biology and Ecology*, 379(1–2), 28–33. https://doi.org/10.1016/j.jembe.2009.08.012

Bax, N., Williamson, A., Aguero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: A threat to global biodiversity. *Marine Policy*, 27(4), 313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Behrens Yamada, S., & G. Boulding, E. (1998). Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology*, 220(2), 191–211. https://doi.org/10.1016/S0022-0981(97)00122-6

Blundon, J. A., & Kennedy, V. S. (1982). Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *Journal of Experimental Marine Biology and Ecology*, 65(1), 47–65. https://doi.org/10.1016/0022-0981(82)90175-7

Boulding, E. G. (1984). Crab-resistant features of shells of burrowing bivalves: Decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology*, 76(3), 201–223. https://doi.org/10.1016/0022-0981(84)90189-8

Boyle, T., Keith, D., & Pfau, R. (2010). Occurrence, reproduction, and population genetics of the estuarine mud crab, *Rhithropanopeus harrisii* (Gould) (Decapoda, Panopidae) in Texas freshwater reservoirs. *Crustaceana*, 83(4), 493–505. https://doi.org/10.1163/001121610X492148

Bradley, T. J. (2008). Hyper-regulators: life in fresh water. In T. J. Bradley (Ed.), *Animal Osmoregulation* (pp. 83-95). Lancaster: MTP.

Campbell, R. T., Baring, R. J., & Dittmann, S. (2019). Cracking the cuisine: Invasive European shore crabs (*Carcinus maenas*) select a menu of soft-shelled mussels over cockles. *Journal of Experimental Marine Biology and Ecology*, 517, 25–33. https://doi.org/10.1016/j.jembe.2019.05.011

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, 89(4), 932–949. https://doi.org/10.1111/brv.12087

Christiansen, M. E., & Costlow, J. D. (1975). The effect of salinity and cyclic temperature on larval development of the mud-crab *Rhithropanopeus harrisii* (Brachyura: Xanthidae) reared in the laboratory. *Marine Biology*, 32(3), 215–221. https://doi.org/10.1007/BF00399201

Costlow, J. D., Bookhout, C. G., & Monroe, R. J. (1966). Studies on the Larval Development of the Crab,

Rhithropanopeus harrisii (Gould). I. The Effect of Salinity and Temperature on Larval Development. *Physiological Zoology*, 39(2), 81–100. https://doi.org/10.1086/physzool.39.2.30152421

Crane, J. (1975). *Fiddler Crabs of the World. Ocypodidae: Genus Uca*. Princeton, NJ: Princeton University Press, pp. 736.

Czerniejewski, P. (2009). Some aspects of population biology of the mud crab, *Rhithropanopeus harrisii* (Gould, 1841) in the Odra estuary, Poland. *Oceanological and Hydrobiological Studies*, 38(4), 49-62. https://doi.org/10.2478/v10009-009-0043-3

Czerniejewski, P., & Rybczyk, A. (2008). Body weight, morphometry, and diet of the mud crab, *Rhithropanopeus harrisii tridentatus* (Maitland, 1874) in the Odra estuary, Poland. *Crustaceana*, 81(11), 1289–1299. https://doi.org/10.1163/156854008X369483

Davenport, J. (1979). The isolation response of mussels (*Mytilus edulis* l.) exposed to galling sea-water concentrations. *Journal of the Marine Biological Association of the United Kingdom*, 59(1), 123–132. https://doi.org/10.1017/S0025315400046221

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution*, 20(9), 470–474. https://doi.org/10.1016/j.tree.2005.07.006

Diamond, D. W., Scott, L. K., Forward Jr, R. B. and Kirby-Smith, W. (1989). Respiration and osmoregulation of the estuarine crab, *Rhithropanopeus harrisii* (Gould): effects of the herbicide, alachlor. *Comparative Biochemistry and Physiology*, 93(2), 313–318.

Elmgren, R., & Hill, C. (1997). Ecosystem function at low biodiversity – the Baltic example. In C. Tickell (Aut.), R. Ormond, J. Gage, M. Angel (Eds.), *Marine Biodiversity: Patterns and Processes* (pp. 319-336). Cambridge: Cambridge University Press.

Elner, R. W. (1980). The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Marine Behaviour and Physiology*, 7(1), 15–24. https://doi.org/10.1080/10236248009386968

Evans, D. H., Piermarini, P. M., & Choe, K. P. (2005). The multifunctional fish gill: Dominant site of gas exchange, osmoregulation, acid-base regulation, and excretion of nitrogenous waste. *Physiological Reviews*, 85(1), 97–177. https://doi.org/10.1152/physrev.00050.2003

Falster, D. S., Warton, D. I. & Wright, I. J. (2006). SMATR: Standardised major axis tests and routines, ver 2.0. <http://www.bio.mq.edu.au/ecology/SMATR/>

Finnish Environment Institute (2020). *Sea surface salinity*. Retrieved April 10, 2020, from <https://wwwp.ymparisto.fi/kartta/>

Forsström, T., Ahmad, F., & Vasemägi, A. (2017). Invasion genomics: genotyping-by-sequencing approach reveals regional genetic structure and signatures of temporal selection in an introduced mud crab. *Marine Biology*, 164(9), 1–11. https://doi.org/10.1007/s00227-017-3210-1

Forsström, T., Fowler, A. E., Manninen, I., & Vesakoski, O. (2015). An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisii* in the Northern Baltic Sea. *Biological Invasions*, 17(9). https://doi.org/10.1007/s10530-015-0909-0

Forsström, T., Vesakoski, O., Riipinen, K., & Fowler, A. E. (2018). Post-invasion demography and persistence of a novel functional species in an estuarine system. *Biological Invasions*, 20(11), 3331–3345. https://doi.org/10.1007/s10530-018-1777-1

Fowler, A. E., Forsström, T., von Numers, M., & Vesakoski, O. (2013). The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: Distribution and ecology.

Aquatic Invasions, 8(1), 89-96. https://doi.org/10.3391/ai.2013.8.1.10

Freire, C. A., Onken, H., & McNamara, J. C. (2008). A structure-function analysis of ion transport in crustacean gills and excretory organs. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, 151(3), 272–304). https://doi.org/10.1016/j.cbpa.2007.05.008

Fritts, T. H., & Rodda, G. H. (1998). The role of introduced species in the degradation of island ecosystems: A case history of Guam. *Annual Review of Ecology and Systematics*, 29, 113–140. https://doi.org/10.1146/annurev.ecolsys.29.1.113

Furman, E., Pihlajamäki, M., Välipakka, P. & Myrberg, K. (2014). The Baltic Sea Environment and Ecology. Finnish Environment Institute.

Goldschmidt, T., Witte, F., & Wanink, J. (1993). Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology*, 7(3), 686–700. https://doi.org/10.1046/j.1523-1739.1993.07030686.x

Grzesiuk, M. & Mikulski, A. (2006). The effect of salinity on freshwater crustaceans. *Polish Journal of Ecology*, 54(4), 4-669.

Hegele-Drywa, J., & Normant, M. (2014). Effect of temperature on physiology and bioenergetics of adult Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) from the southern Baltic Sea. *Oceanological and Hydrobiological Studies*, 43(3), 219-227. https://doi.org/10.2478/s13545-014-0136-9

Hegele-Drywa, J., Normant, M., Szwarc, B. & Podłuska, A. (2014). Population structure, morphometry and individual condition of the non-native crab *Rhithropanopeus harrisii* (Gould, 1841), a recent coloniser of the Gulf of Gdańsk (southern Baltic Sea), *Oceanologia*, 56,(4), 805-824. https://doi.org/10.5697/oc.56-4.805

HELCOM (2012). Observed non-indegenous and cryptogenic species in the Baltic Sea. HELCOM Baltic Sea Environment Fact Sheet 2012. <http://www.helcom.fi/baltic-sea-trends/environment-fact-sheets/biodiversity/observed-non-indegenous-and-cryptogenic-species-in-the-baltic-sea>

HELCOM (2013). Climate Change in the Baltic Sea Area – HELCOM Thematic Assessment in 2007. Baltic Sea Environment Proceedings No. 137. Helsinki Commission. <http://helcom.fi/Lists/Publications/BSEP137.pdf>

Henry, R. P., Lucu, Č., Onken, H., & Weihrauch, D. (2012). Multiple functions of the crustacean gill: Osmotic/ionic regulation, acid-base balance, ammonia excretion, and bioaccumulation of toxic metals. *Frontiers in Physiology*, 3(431), 431. https://doi.org/10.3389/fphys.2012.00431

Herrick, F. J. (1895). The American lobster: a study of its habits and development. *Fishery Bulletin*, 15, 1-252.

Heuring, W. L., & Hughes, M. (2019). It takes two: Seasonal variation in sexually dimorphic weaponry results from divergent changes in males and females. *Ecology and Evolution*, 9(9), 5433–5439. https://doi.org/10.1002/ece3.5136

Holopainen, R., Lehtiniemi, M., Meier, H. E. M., Albertsson, J., Gorokhova, E., Kotta, J., & Viitasalo, M. (2016). Impacts of changing climate on the non-indigenous invertebrates in the northern Baltic Sea by end of the twenty-first century. *Biological Invasions*, 18, 3015–3032. https://doi.org/10.1007/s10530-016-1197-z

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. https://doi.org/10.1890/04-0922

Hughes, R., & Seed, R. (1981). Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Marine Ecology Progress Series*, 6, 83–89. https://doi.org/10.3354/meps006083

Huxley, J. S. (1932). *Problems of relative growth*. New York, NY: Lincoln Mac Veag - The Dial Press.

IUCN (2019). *Invasive alien species*. Retrieved November 20, 2019, from <https://www.iucn.org/regions/europe/our-work/species/invasive-alien-species>

Jormalainen, V., Gagnon, K., Sjöroos, J. & Rothäusler, E. (2016). The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biological Invasions*, 18(5), 1409-1419.

Juanes, F. (1992). Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series*, 87(3), 239-249.

Kaplan, E. L., & Meier, P. (1958). Nonparametric Estimation from Incomplete Observations. *Journal of the American Statistical Association*, 53(282), 457-481.

Karhilahti, A. (2010). Taskurapu tarttui pyydykseen. *Suomen luonto*, 4, 12–13.

Kassambara, A., Kosinski, M. & Biecek, P. (2019). survminer: Drawing Survival Curves using 'ggplot2'. R package version 0.4.6. <https://CRAN.R-project.org/package=survminer>

Kautsky, N. (1981). On the trophic role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. *Kieler Meeresforsch Sonderh*, 5, 454–461.

Kautsky, N., Johannesson, K. & Tedengren, M. (1990). Genotypic and phenotypic differences between Baltic and North Sea Populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and Morphology. *Marine Ecology Progress Series*, 59(3), 203-210.

Kotta, J., Wernberg, T., Jänes, H., Kotta, I., Nurkse, K., Pärnoja, M. & Orav-Kotta, H. (2018). Novel crab predator causes marine ecosystem regime shift. *Scientific Reports*, 8(1).

Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In J. R. Krebs, N. B. Davies (Eds.), *Behavioural Ecology, an Evolutionary Approach* (pp. 23–63). Sunderland, MA: Sinauer.

Kumlu, M., Jones, D. A. (1995). Salinity tolerance of hatchery-reared postlarvae of *Penaeus indicus* H. Milne Edwards originating from India. *Aquaculture*, 130(2-3), 287–296.

Lang, F., Govind, C. K., & Costello, W. J. (1978). Experimental transformation of muscle fiber properties in lobster. *Science*, 201(4360), 1037–1039. https://doi.org/10.1126/science.684425

Larsen, E. H., Deaton, L. E., Onken, H., O'Donnell, M., Grosell, M., Dantzler, W. H., & Weihrauch, D. (2014). Osmoregulation and Excretion. *Comprehensive Physiology*, 4, 405–573. https://doi.org/10.1002/cphy.c130004

Laughlin, R. B., & French, W. (1989). Differences in responses to factorial combinations of temperature and salinity by zoeae from two geographically isolated populations of the mud crab *Rhithropanopeus harrisii*. *Marine Biology*, 102(3), 387–395. https://doi.org/10.1007/BF00428491

Lawton, P., & Hughes, R. (1985). Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. *Marine Ecology Progress Series*, 27, 143–154. https://doi.org/10.3354/meps027143

Lee, S. Y. (1993). Chela height is an acceptable indicator of chela strength in *Carcinus maenas* (Linnaeus, 1758) (Decapoda, Brachyura). *Crustaceana*, 65(1), 115–116. https://doi.org/10.1163/156854093X00450

Lee, S. Y., & Seed, R. (1992). Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series*, 84,151–160)

https://doi.org/10.2307/24829550

MacDougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86(1), 42–55. https://doi.org/10.1890/04-0669

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10(3), 689–710.

Mariappan, P., Balasundaram, C. & Schmitz, B. (2000). Decapod Crustacean Chelipeds: an Overview. *Journal of Bioscience*, 25(3), 301-13.

Mascaró, M., & Seed, R. (2001). Choice of prey size and species in *Carcinus maenas* (L.) feeding on four bivalves of contrasting shell morphology. *Hydrobiologia*, 449, 159–170. https://doi.org/10.1023/A:1017569809818

Matheson, K., McKenzie, C., Gregory, R., Robichaud, D., Bradbury, I., Snelgrove, P., & Rose, G. (2016). Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. *Marine Ecology Progress Series*, 548, 31–45. https://doi.org/10.3354/meps11674

McLay, C. (2015). Moulting and growth in Brachyura. *The Crustacea, Treatise on Zoology – Anatomy Taxonomy, Biology*, 9, 245-316.

Meier, H. E. M., Kjellström, E., & Graham, L. P. (2006). Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. *Geophysical Research Letters*, 33(15), L15705. https://doi.org/10.1029/2006GL026488

Meinesz, A., Belsher, T., Thibaut, T., Antolic, B., Mustapha, K. Ben, Boudouresque, C. F., Chiaverini, D., Cinelli, F., Cottalorda, J. M., Djellouli, A., El Abed, A., Orestano, C., Grau, A. M., Ivesa, L., Jaklin, A., Langar, H., Massuti-Pascual, E., Peirano, A., Tunesi, L., de Vaugelas, J., Zavodnik, N. & Zuljevic, A. (2001). The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. *Biological Invasions*, 3(2), 201–210. https://doi.org/10.1023/A:1014549500678

Milke, L. M., & Kennedy, V. S. (2005). Mud crabs (Xanthidae) in Chesapeake Bay: claw characteristics and predation on epifaunal bivalves. *Invertebrate Biology*, 120(1), 67-77. https://doi.org/10.1111/j.1744-7410.2001.tb00027.x

Murray, L. G., Seed, R., & Jones, T. (2007). Predicting the impacts of *Carcinus maenas* predation on cultivated *Mytilus edulis* beds. *Journal of Shellfish Research*, 26(4), 1089–1098. https://doi.org/10.2983/0730-8000(2007)26[1089:ptiocm]2.0.co;2

Nagarajan, R., Lea, S. E. G., & Goss-Custard, J. D. (2006). Seasonal variations in mussel, *Mytilus edulis* L. shell thickness and strength and their ecological implications. *Journal of Experimental Marine Biology and Ecology*, 339(2), 241–250. https://doi.org/10.1016/j.jembe.2006.08.001

Normant, M. & Gibowicz, M. (2008). Salinity induced changes in haemolymph osmolality and total metabolic rate of the mud crab *Rhithropanopeus harrisii* Gould, 1841 from Baltic coastal waters. *Journal of Experimental Marine Biology and Ecology*, 355, 145–152.

Normant, M., Kubicka, M., Lapucki, T., Czarnowski, W., & Michalowska, M. (2005). Osmotic and ionic haemolymph concentrations in the Baltic Sea amphipod *Gammarus oceanicus* in relation to water salinity. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, 141(1), 94–99. https://doi.org/10.1016/j.cbpb.2005.04.007

Normant, M., & Lamprecht, I. (2006). Does scope for growth change as a result of salinity stress in the amphipod *Gammarus oceanicus*? *Journal of Experimental Marine Biology and Ecology*, 334(1), 158–163. https://doi.org/10.1016/j.jembe.2006.01.022

Occhipinti-Ambrogi, A., & Savini, D. (2003). Biological invasions as a component of global change in

stressed marine ecosystems. *Marine Pollution Bulletin*, 46(5), 542–551). https://doi.org/10.1016/S0025-326X(02)00363-6

Occhipinti-Ambrogi, A. (2007). Global change and marine communities: Alien species and climate change. *Marine Pollution Bulletin*, 55(7–9), 342–352. https://doi.org/10.1016/j.marpolbul.2006.11.014

Paavola, M., Olenin, S., & Leppäkoski, E. L. (2005). Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science*, 64(4), 738-750. https://doi.org/10.1016/j.ecss.2005.03.021

Paolucci, E. M., MacIsaac, H. J., & Ricciardi, A. (2013). Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, 19(8), 988–995. https://doi.org/10.1111/ddi.12073

Pickering, T., & Quijón, P. A. (2011). Potential effects of a non-indigenous predator in its expanded range: Assessing green crab, *Carcinus maenas*, prey preference in a productive coastal area of Atlantic Canada. *Marine Biology*, 158(9), 2065–2078. https://doi.org/10.1007/s00227-011-1713-8

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52, 137–154.

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, 7(9), 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Riisgård, H., Larsen, P., Turja, R., & Lundgreen, K. (2014). Dwarfism of blue mussels in the low saline Baltic Sea—growth to the lower salinity limit. *Marine Ecology Progress Series*, 517, 181–192. https://doi.org/10.3354/meps11011

Rivera-Ingraham, G. A., & Lignot, J. H. (2017). Osmoregulation, bioenergetics and oxidative stress in coastal marine invertebrates: Raising the questions for future research. *Journal of Experimental Biology*, 220(10), 1749–1760). https://doi.org/10.1242/jeb.135624

Ruscoe, I. M., Shelley, C. C., Williams, G. R. (2004). The combined effects of temperatureand salinity on growth and survival of juvenile mud crabs (*Scylla serrata*). *Aquaculture*, 238, 239–247.

Ryan, E. (1956). Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. *The American Midland Naturalist*, 56(1), 138-162. doi:10.2307/2422450.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., & Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, 32, 305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences*, 274(1615), 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Schenk, S. C., & Wainwright, P. C. (2001). Dimorphism and the functional basis of claw strength in six brachyuran crabs. *Journal of Zoology*, 255(1), 105–119. https://doi.org/10.1017/S0952836901001157

Schoener, T. W. (1971). A theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369–404.

Schubert, K. (1936). *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. *Zoologischer Anzeiger*, 116, 320-323.

Seed, R. (1980). Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (=*Modiolus*) *demissa*. *Estuarine and*

Coastal Marine Science, 11(4), 445–458. https://doi.org/10.1016/S0302-3524(80)80067-3

Seed, R., & Hughes, R. N. (1995). Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology*, 193(1–2), 177–195. https://doi.org/10.1016/0022-0981(95)00117-4

Seed, R. (1993). Invertebrate predators and their role in structuring coastal and estuarine populations of filter feeding bivalves. In R. F. Dame (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes (pp. 149–195). Heidelberg: Springer-Verlag. https://doi.org/10.1007/978-3-642-78353-1_5

Silverman, H. G., & Roberto, F. F. (2010). Byssus formation in *Mytilus*. In J. von Byern, I. Grunwald (Eds.), *Biological Adhesive Systems* (pp. 273–283). Vienna: Springer. https://doi.org/10.1007/978-3-7091-0286-2_18

Smith, L. D., & Palmer, A. R. (1994). Effects of manipulated diet on size and performance of brachyuran crab claws. *Science*, 264(5159), 710–712. https://doi.org/10.1126/science.264.5159.710

Smyth, K., & Elliott, M. (2016). Effects of changing salinity on the ecology of the marine environment. In M. Solan, N. Whiteley (Eds.), *Stressors in the Marine Environment* (pp. 161–174). Oxford UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198718826.003.0009

Stein, R. A. (1976). Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. *Canadian Journal of Zoology*, 54(2), 220–227. https://doi.org/10.1139/z76-024

Therneau, T. (2015). A Package for Survival Analysis in S. version 2.38, <https://CRAN.R-project.org/package=survival>.

Turoboyski, K. (1973). Biology and ecology of the crab *Rhithropanopeus harrisii* ssp. *tridentatus*. *Marine Biology*, 23, 303–313. http://dx.doi.org/10.1007/BF00389338

Verhoeven, K. J. F., Biere, A., Harvey, J. A., & Van Der Putten, W. H. (2009). Plant invaders and their novel natural enemies: Who is naïve? *Ecology Letters*, 12(2), 107–117. https://doi.org/10.1111/j.1461-0248.2008.01248.x

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325), 494–499. https://doi.org/10.1126/science.277.5325.494

Vuorinen, I., Antsulevich, A. E., & Maximovich, N. V. (2002). Spatial distribution and growth of the common mussel *Mytilus edulis* L. in the archipelago of SW-Finland, northern Baltic Sea. *Boreal Environment Research*, 7(1).

Vuorinen, I., Hänninen, J., Rajasilta, M., Laine, P., Eklund, J., Montesino-Pouzols, F., Corona, F., Junker, K., Meier, H. E. M., & Dippner, J. W. (2015). Scenario simulations of future salinity and ecological consequences in the Baltic Sea and adjacent North Sea areas-implications for environmental monitoring. *Ecological Indicators*, 50, 196–205. https://doi.org/10.1016/j.ecolind.2014.10.019

Warner, G. F., Chapman, D., Hawkey, N., & Waring, D. G. (1982). Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). *Journal of Zoology*, 196(4), 431–438. https://doi.org/10.1111/j.1469-7998.1982.tb03514.x

Warner, G. F., & Jones, A. R. (1976). Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology*, 180(1), 57–68. https://doi.org/10.1111/j.1469-7998.1976.tb04663.x

Westerbom, M., Kilpi, M., & Mustonen, O. (2002). Blue mussels, *Mytilus edulis*, at the edge of the range: Population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. *Marine Biology*, 140(5), 991–999. https://doi.org/10.1007/s00227-001-0765-6

Winberg, G. G. (1960). Rate of metabolism and food requirements of fishes. *Fisheries Research Board of Canada (Translation Series)*, 194, 1–202.

Ye, L., Jiang, S., Zhu, X., Yang, Q., Wen, W. & Wu, K. (2009). Effects of salinity on growth and energy budget of juvenile *Penaeus monodon*. *Aquaculture*, 290, 140–144.

8. Appendices

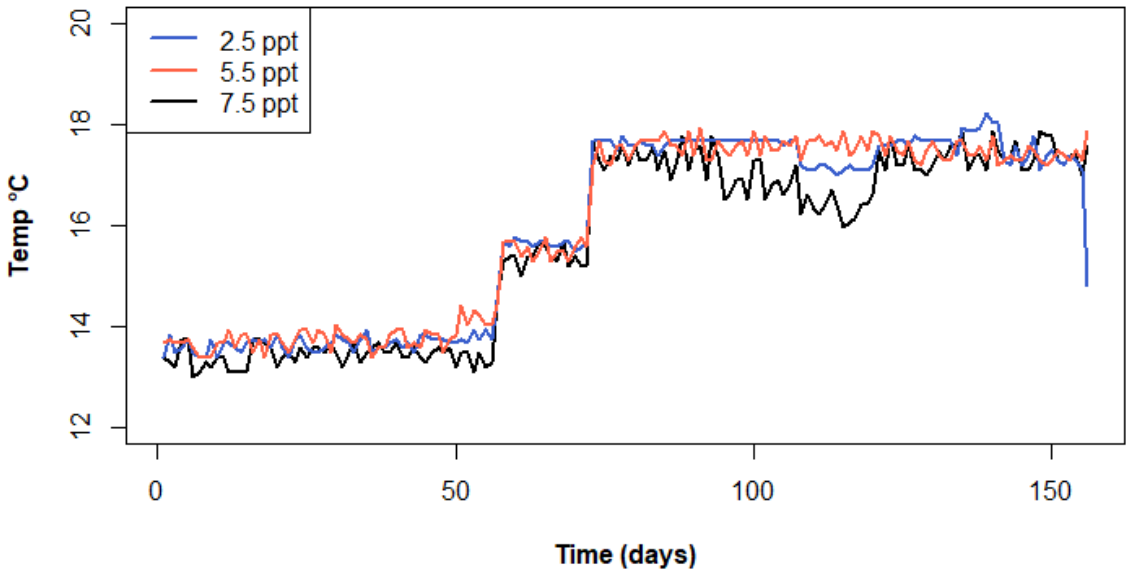

Figure 1. Temperature during the salinity experiment recorded with Onset's HOBO pedant data loggers. Temperatures are from three aquariums of which each belonged to individual water recirculation system assigned to one of the three salinity levels (2.5, 5.5 and 7.5 ppt). Between days 57 and 73 temperature was adjusted gradually from 13 °C to 17 °C.

Table 1. Range and mean values of the morphological dimensions (mm) of the mud crabs by sex and treatment group. Dimensions: carapace width (CW), crusher claw height (CRH), crusher claw length (CRL), cutter claw height (CUH), cutter claw length (CUL), body weight (BW).

Sex	Treatment (ppt)	Dimension	n	Range	Mean	SD
Female	2.5	CW	9	10.11 - 13.04	11.18	0.94
		CRH	9	3.45 - 4.62	3.88	0.42
		CRL	9	6.53 - 8.31	7.25	0.68
		CUH	9	2.67 - 3.53	3.06	0.29
		CUL	9	5.51 - 7.37	6.42	0.61
		BW	8	0.4 - 0.68	0.52	0.11
	5.5	CW	9	10.25 - 14.13	11.94	1.65
		CRH	9	3.63 - 5.24	4.26	0.57
		CRL	9	6.73 - 9.51	7.79	1.09
		CUH	9	2.86 - 3.99	3.39	0.43
		CUL	9	5.54 - 8.7	6.98	1.00
		BW	8	0.43 - 1.07	0.68	0.26
	7.5	CW	10	9.81 - 13.25	12.06	1.05
		CRH	10	3.335 - 4.66	4.08	0.44
		CRL	10	6.34 - 8.66	7.62	0.72
		CUH	10	2.66 - 3.72	3.27	0.30
		CUL	9	5.49 - 7.72	6.81	0.59
		BW	9	0.36 - 0.85	0.66	0.14
Male	2.5	CW	23	8.71 - 20.37	14.47	3.52
		CRH	23	3.06 - 10.45	6.49	2.11
		CRL	23	6.06 - 19.03	11.83	3.80
		CUH	23	2.61 - 7.9	4.98	1.59
		CUL	23	4.84 - 15.65	10.36	3.18
		BW	13	0.41 - 4.18	1.84	1.21
	5.5	CW	48	7.78 - 21.96	15.90	3.72
		CRH	48	2.83 - 10.84	7.17	2.24
		CRL	49	5.06 - 20.36	13.10	4.00
		CUH	49	2.25 - 8.71	5.64	1.69
		CUL	48	4.8 - 17.32	11.38	3.34
		BW	34	0.2 - 4.62	1.83	1.25
	7.5	CW	30	6.64 - 21.09	14.62	3.84
		CRH	30	2.23 - 10.28	6.48	2.28
		CRL	30	4.22 - 18.7	11.81	3.96
		CUH	30	1.83 - 7.89	4.97	1.72
		CUL	30	3.95 - 15.95	10.37	3.39
		BW	15	0.12 - 3.7	1.59	1.25

Table 2. Range and mean values of the morphological dimension (mm or g) of the mud crabs included to the critical prey size data analyses. Dimensions: carapace width (CW), crusher claw height (CRH), crusher claw length (CRL), cutter claw height (CUH), cutter claw length (CUL), body weight (BW).

Sex	n	Dimension	Range	Mean ± SD
Female	26	CW	8.61 - 17.87	13.52 ± 2.61
		CRH	2.85 - 6.5	4.74 ± 1.03
		CRL	5.64 - 12.69	9.04 ± 1.97
		CUH	2.31 - 5.35	3.81 ± 0.80
		CUL	5.07 - 11.39	8.12 ± 1.82
		BW	0.29 - 2.29	1.03 ± 0.53
Male	56	CW	8.41 - 21.21	14.84 ± 3.81
		CRH	2.74 - 10.83	6.57 ± 2.23
		CRL	5.56 - 20.04	12.05 ± 3.96
		CUH	2.15 - 8.06	5.03 ± 1.62
		CUL	4.72 - 17.55	10.58 ± 3.41
		BW	0.24 - 4.38	1.71 ± 1.2